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THE FRESHWATER MOLLUSCS OF THE CANADIAN INTERIOR BASIN

Arthur H. Clarke

National Museum of Natural Sciences, National Museums of Canada, Ottawa, Canada

ABSTRACT

The Canadian Interior Basin encompasses both the " Hudson Bay Basin " and the Canadian part of the " Arctic Basin " of previous authors. It comprises more than 1/3 of North America. Taxonomic revision of the freshwater molluscs found in it, based principally on a biometric population analysis, has resulted in the recognition of 37 genera and subgenera and 103 species and subspecies.

The Introduction contains summaries of previous work, topography, geology, Pleistocene history, existing connections between drainage areas, phytogeographic regions, climate, and field methods used. This is followed by a discussion of the post-Pleistocene origins of the fauna, some observed relationships of zoogeography with temperature and with geology, and the extent of distributional equilibrium that has been achieved. The Systematic Section contains discussions of the taxonomy, morphology (with statistical summaries), zoogeography, biology, ecology, and interspecific relationships of all species and subspecies. Simplified identification keys and distribution maps and illustrations (many in colour) are included for all species and subspecies. Numerous taxonomic changes are recommended and the following new names are proposed: **Herringtonium** (new subgenus of *Sphaerium*) and **Physa jennessi athearni** (n. ssp.).

I. INTRODUCTION

Scope

The Canadian Interior Basin comprises more than $\frac{1}{3}$ of North America. It extends from the western boundary of the Atlantic Coastal Plain to the Rocky Mountains and from the Arctic Ocean to the northern boundaries of the drainage basins of the St. Lawrence, Mississippi and Missouri rivers. It covers most of Canada and extends into 5 states of the United States. It is defined by the combined boundaries of the drainage basins of the rivers and streams that flow into James Bay, Hudson Bay and into all other marine waters from Cape Chidley, Labrador, to the mouth of Firth River, Yukon Territory, and all drainage basins in the Northwest Territories. The name " Canadian Interior Basin " as here proposed embraces the areas of the Hudson Bay Basin and the Canadian part of the Arctic Basin (see *Canada Year Book*, 1968: 9) and combines them into a single unit. See front end-paper.

The purposes of the present work are: (1) to provide keys, illustrations, and descriptions for the identification of the 103 species and subspecies of freshwater molluscs here recognized that inhabit this region; (2) to evaluate the classical and other taxonomic characters, using the biometric population approach; (3) to determine regional geographical distributions and suggest limiting factors; (4) to revise the systematics of the taxonomic groups and (5) to discuss aspects of the biology, ecology, and intraspecific associations of these freshwater molluscs.

Acknowledgements

Whatever degree of success has been achieved is due in large measure to the generous assistance of numerous friends and colleagues. My wife, Louise, and my son, Arthur, provided cheerful and productive assistance in the field during several summers. Mr. H. D. Athearn of Cleveland, Tennessee, collected with me in 1963 and 1967 and collected independently in 1965 with great success on each occasion. Mrs. Elizabeth Macpherson collected for two months in 1961 in the vicinity of Aberdeen Lake, N.W.T., specifically for this study. Mr. L. M. Marhue ably assisted in both field and laboratory work from 1965 to 1967. Rev. H. B. Herrington assisted for many years by sorting field collections and by identifying the Sphaeriidae. Mrs. Muriel F. I. Smith provided expert laboratory assistance from 1966 to 1970 and Mrs. Jane Topping helped in many similar ways from 1967 to 1970.

The following people also deserve special thanks: Mr. M. K. Jacobson, Dr. W. H. Heard, Dr. Irene Lubinsky, Dr. D. E. McAllister, the late Mr. W. H. Van Vliet, and Miss Marjory Athearn for field assistance; Mrs. Joyce Cook, and Mr. F. R. Cook for making important supplementary collections for this study; Dr. D. R. Oliver, Dr. Richard Hartland-Rowe, Dr. R. W. Coleman, and Mr. Marcel Ouellet for donating very substantial material from the research area; and Mrs. Raye Munroe, Mrs. Marilee Egan, Miss Helen Bradbury, and Miss Katharine Knoké for much competent laboratory assistance.

Most of the collections available from previously inaccessible arctic parts of the Northwest Territories were provided by the Arctic Research Branch of the Fisheries Research Board. Without those priceless collections this report would be much less complete. Much additional material from Great Slave Lake, Lake Athabasca, and other northern localities was generously donated by Dr. J. G. Oughton. Valuable Pleistocene collections that help to document the Beringian survival of freshwater species during the Wisconsin were collected by Mr. C. R. Harington and submitted by Dr. Jaan Terasmae. Useful collections from a number of northern Ontario lakes were also made available by the Ontario Department of Lands and Forests. The many other collectors, past and present, who have provided material are cited in the text.

Several curators have kindly lent material or have allowed access to collections in connection with this study. These are Dr. Joseph Rosewater, Dr. Harald Rehder, and Dr. J. P. E. Morrison of the United States National Museum; Dr. William J. Clench and Dr. Kenneth E. Boss of the Museum of Comparative Zoology; Dr. R. Tucker Abbott of the Academy of Natural Sciences of Philadelphia; Dr. J. B. Burch and Dr. Henry van der Schalie of the Museum of Zoology, University of Michigan; Dr. William K. Emerson and Mr. William Old of the American Museum of Natural History; and Dr. Samuel B. Eddy of the University of Minnesota.

Parts of the manuscript were read by Dr. Harold J. Walter, (Lymnaeidae), Rev. H. B. Herrington (Sphaeriidae), Dr. Carol B. Stein, Dr. Joseph Rosewater, and Mr. Richard I. Johnson (Unionidae). Although I did not necessarily agree with all their comments, the text was improved by consideration of their remarks.

The illustrations were prepared by Messrs. John Tottenham, Robert Thompson, and Charles Douglas, all former or present staff artists of the National Museum of Natural Sciences.

Special debts of gratitude are owing to three distinguished colleagues, Dr. Aurèle La Rocque, Dr. Alan Mozley, and Rev. Dr. H. B. Herrington whose previous extensive and careful works have been drawn on constantly in the course of this study. Their researches, and the works of 2 outstanding malacologists of a previous generation, Frank Collins Baker and William Healey Dall, have provided the principal foundation of knowledge on which the present work has been based.

Finally I wish to thank the National Museum of Natural Sciences for generously providing me with the necessary field, laboratory, and artistic support since 1959, which made possible the completion of this work.

Previous Work

The history of malacological work concerning the Canadian Interior Basin is closely interwoven with the history of malacology in Canada. This has been recently summarized by La Rocque (1962) and will not be repeated here. Drake (1963) has provided a useful history of non-marine malacological work in British Columbia which is also pertinent.

Famous 19th century Canadian malacologists noted for their interest in freshwater faunas were Robert Bell, George M. Dawson, Francis R. Latchford, George W. Taylor, and Joseph F. Whiteaves. Some of their publications are cited

here and complete lists of their malacological works are given in La Rocque (1953). Much of the Bell Collection and nearly all the Whiteaves Collection are now in the National Museum of Natural Sciences. The Latchford Collection and other early collections were formerly in the Royal Ontario Museum and are now in the Museum of Zoology, University of Michigan. The Dawson and Taylor collections no longer exist.

Other 19th century workers whose researches contributed to knowledge of species in the Canadian Interior Basin were Thomas Say, C. S. Rafinesque, Isaac Lea, T. A. Conrad, S. S. Haldeman, G. W. Tryon, A. A. Gould, and J. G. Anthony. Several of their works are also cited here.

During the first half of the present century many other malacologists made substantial contributions. Those who published most extensively on this fauna are: F. C. Baker, W. H. Dall, H. B. Herrington, Aurèle La Rocque, and Alan Mozley. Other workers also contributed but they were principally concerned with other faunas or with other taxonomic groups. These are: H. B. Baker, E. G. Berry, W. J. Clench, Charlotte Dawley, L. S. Frierson, Calvin Goodrich, Junius Henderson, A. E. Ortmann, John Oughton, H. A. Pilsbry, L. S. Russell, C. T. Simpson, Victor Sterki, Bryant Walker, Henry van der Schalie, and Mina Winslow.

In short, competent research on the systematics, zoogeography, evolution, and biology of the freshwater molluscs of North America and of the Canadian Interior Basin has been going on for 150 years. However, for freshwater molluscs there is still nothing comparable to H. A. Pilsbry's *Land Mollusca of North America* or to R. T. Abbott's *American Seashells*. During the past 60 years the only North American works published which contain descriptions or illustrations of entire molluscan faunas are those which cover relatively small geographical areas, and *none* of these areas are in the Canadian Interior Basin.

The only illustrated, general work on all freshwater molluscs of boreal North America is Dall's Harriman Expedition report published in 1905. In addition to being much out-of-date this work contains no descriptions or distribution maps and its illustrations are entirely inadequate.

The most important and useful work on a neighbouring fauna is F. C. Baker's *Fresh Water Mollusca of Wisconsin* published in 1928. Baker recognized scores of " varieties ", " forms ", " races ", and subspecies and designated them *all* by trinomials, following the practice of that period. Most of these, and many of his species also, are biologically invalid as distinct taxonomic units. Students who attempt to identify species or subspecies by applying Baker's criteria therefore become confused and frustrated.

Another useful regional work is *The Mollusca of the Niagara Frontier Region* by Robertson & Blakeslee (1948). This considers a different fauna but, following Baker, it also recognized too many taxa.

Several modern works on Pleistocene shells exist (e.g., Taylor, 1960, 1966; Hibbard & Taylor, 1960, La Rocque, 1966–68) which are also of value in the identification of Recent species. Unfortunately they treat only faunas in the United States which are not closely related to those of the Canadian Interior Basin. Furthermore some of those studies rely too heavily on the overly-divided taxonomic categories of F. C. Baker.

A number of excellent monographs of individual families are also available. Good examples of these are by F. C. Baker (1911, Lymnaeidae; 1945, Planorbidae), Bengt Hubendick (1951, Lymnaeidae; 1962, Acroloxidae), E. G. Berry (1943, North American Hydrobiidae), and P. F. Basch (1963a, North American

Acroloxus and Ancylidae). However, some of them are out of date and many are difficult to obtain.

The necessity for an easily available, modern, and comprehensive work on all freshwater molluscs of the Canadian Interior Basin is clearly evident. Such a work should also facilitate identification of the species and subspecies. Proper identification is the fundamental requisite for further use of the literature and for the effective utilization of molluscs in basic and applied biology, for example in the recognition and control of water pollution, for resource management, and for solution of problems in medical malacology. It is hoped that the present work will contribute to the fulfilment of this need.

Topography and Geology*

The most characteristic feature of the Canadian Interior Basin is the Canadian Shield. This rugged, ancient, mineral-rich plateau extends from the Atlantic Coast of Labrador all the way to Minnesota, Saskatchewan, the Western Arctic Mainland, and Baffin Island. Its approximate western boundary is indicated by the well-known lakes that lie across its border: Lake Winnipeg, Lac la Ronge, Lake Athabasca, Great Slave Lake and Great Bear Lake.

Lakes and rivers abound in this vast region and numerous species of freshwater molluscs are very common. The Canadian (or Precambrian) Shield is unsuitable for some species, however, because of the scarcity of the calcium carbonate necessary for the proper development of their shells. Four main sources of calcium carbonate do exist, i.e., the scattered Proterozoic deposits, the few widely dispersed patches of Palaeozoic rocks, Pleistocene glacial till, and Pleistocene marine sediments east, south, and northwest of Hudson Bay and along the Arctic Coast between Foxe Basin and Amundsen Gulf, but for several species this is still insufficient. A similar general scarcity of freshwater amphipod species in the Canadian Shield has been noted by Bousfield (1958: 56).

Within the Shield and south of Hudson Bay lies the Hudson Bay Lowland, a wide belt of poorly drained flat land covered with black spruce and muskeg. Surface outcrops are of Ordovician to Devonian age. These rocks and widespread Pleistocene marine deposits provide a rich source of calcareous materials for shell growth. Molluscs occur there in great abundance.

West of the Shield and east of the Cordillera are the Interior Plains. This region extends from the Southern United States to the Arctic Ocean. In the Canadian segment flat-bedded bands of progressively younger strata grading from Palaeozoic to Tertiary occur from east to west. Limestone is abundant there and so are freshwater molluscs.

The Cordilleran Region consists of several parallel northwest-trending geological and topographical systems. The most easterly of these, the Rocky, Mackenzie, and Richardson Mountains, extends through western Alberta, eastern British Columbia, western Northwest Territories, and eastern Yukon Territory. Except for the Liard River system in British Columbia and the Peel River system in the Yukon Territory, both of which originate farther west, all river systems in the Canadian Interior Basin rise east of the divide formed by the crest of this mountain system. Bedrock in the Cordilleran Region is of Paleozoic orogenic origin and contains calcium-bearing minerals. Freshwater molluscs are common in this complex zoogeographic region

*See back end-paper map.

and some species and subspecies are of very localized distribution.

The Arctic Archipelago is a geological composite of Precambrian, Paleozoic, Mesozoic, Tertiary, and Quaternary igneous and sedimentary rocks. Freshwater molluscs are known only from two southern regions containing calcareous sediments, i.e., Nettilling Lake on southern Baffin Island and small water bodies on Victoria and Banks islands near their southern edges.

Pleistocene History

Although bedrock geology and surficial topography exert profound influences on the present distribution of freshwater molluscs, Pleistocene events are probably of even greater significance. Each of the 4 major glacial stages, the Nebraskan, Kansan, Illinoian, and Wisconsin, covered nearly all Canada and most of the United States south to Pennsylvania and the Ohio and Missouri River valleys. The fauna indigenous to the glaciated region was wiped out during each of these stages. A few areas north of the southern terminal moraine were not glaciated, at least during the Wisconsin Stage, and some of those areas, as well as the region south of the terminal moraine were certainly refugia for animals and plants. These are (1) a large area in the Yukon Territory and Alaska (the Beringian Refugium), (2) most of Banks Island and part of Melville Island in the Western Arctic, (3) part of the continental shelf off Nova Scotia and New England, and (4) a few isolated areas in southern Saskatchewan, southern Alberta, and Wisconsin.

Wisconsin glacial ice began to recede about 12,000 to 14,000 years B.P. (before present) and, except for remnants in montane regions, by 5,000 B.P. it had nearly vanished. Meltwater formed huge proglacial lakes and their drainage courses provide migration routes for numerous molluscan invaders. The largest of these lakes were Lake Agassiz and Lake Barlow-Ojibway.

Lake Agassiz existed from about 12,000 to 7,000 B.P. and covered a huge area. It extended from Minnesota and North Dakota northwest to Great Bear Lake, a distance of 1,600 miles, and from central Ontario to the Rocky Mountains. Not all this area was covered by water at any one time and the southern part was uncovered by ice and inundated first (see Elson, 1967 and Glacial Map of Canada, 1968).

Lake Agassiz drained south through the River Warren in the valley of the Minnesota River from about 12,000 to 9,500 B.P. Near the end of this period further glacial recession in the north coincident with isostatic uplift in the south brought about use of a more easterly drainage route through Lake Nipigon and into Lake Superior and the St. Lawrence River system. Lake Agassiz may also have been confluent with Lake Barlow-Ojibway during part of this period but opinion varies. The Lake Nipigon outlet was probably active from about 9,000 to 8,300 B.P. Later as ice further diminished, Lake Agassiz drained northeastward by way of the Severn, Hayes, and Nelson River valleys and became reduced in size. Lake Winnipeg, Lake Athabasca, Great Slave Lake, and Great Bear Lake are modern remnants of Lake Agassiz. See Mayer-Oakes (1967) for detailed discussions of many aspects of Lake Agassiz.

Lake Barlow-Ojibway occupied an irregular area about 500 miles long and 150 miles wide which extended from present-day Lac Mistassini and the Eastmain River in Quebec to an area about 75 miles northeast of Lake Superior. It existed from about 8,000 to 6,000 B.P. and drained through the Ottawa River valley into the St. Lawrence River. Further melting of ice in the north

unblocked wide passageways to James Bay and must have caused a sudden and massive reduction in the size of the lake. Surviving remnants of Lake Barlow-Ojibway are Lake Abitibi, Lac Chibougamau, and Lac Mistassini. The clay soils which now characterize the Clay Belt in northern Ontario and Quebec were formed from the fine sediments deposited throughout the basin of Lake Barlow-Ojibway. Baldwin (1958) has described the geology and botany of the Clay Belt in detail.

Other post-Wisconsin confluences may also be significant. For example, during deglaciation the waters of two headwater tributaries of the South Saskatchewan River, the St. Mary and Oldman rivers in southwestern Alberta, were diverted into the Milk River valley and on into the Missouri and Mississippi rivers. As ice receded further the waters of these tributaries again flowed into the South Saskatchewan River which then flowed into the Qu'Appelle River valley and on to the Assiniboine and Red rivers. Later the South Saskatchewan assumed its present northeasterly course leading to the Saskatchewan River and on to Lake Winnipeg and Hudson Bay.

The principal significance of proglacial lakes and lake outlets and of past stream confluences is in developing the present distribution patterns of those species whose migrations between water bodies can only occur, or can best occur, under conditions of confluence (e.g., Unionidae and Viviparidae). For these, postglacial confluences opened (1) wide avenues for immigration of Mississippi-Missouri River basin species into central, western, and northwestern Canada and (2) similar but more restricted avenues for immigration of Great Lakes—St. Lawrence River species, previously or concurrently derived from the Mississippi River basin and the Atlantic Coastal Plain, into northern Ontario and Quebec. Small autogamous species may take advantage of confluences for dispersal but they can also be effectively distributed by passive overland transport (Malone, 1965a, b, 1966). S. J. Tuthill (pers. comm.) has shown that in Alaska many species of small, freshwater molluscs even occur in silt-laden ponds on the tops of glaciers. As pointed out elsewhere (Clarke, 1970b), the ability to be passively transported and the capability for facultative self-fertilization are interdependent features which enable pulmonate gastropods, Valvatidae and Sphaeriidae, to colonize rapidly previously unoccupied geographical areas.

Mention must be made of some post-Pleistocene climatic changes. Pollen studies and researches in other fields have shown that in southeastern Canada a warm period existed from about 6,000 B.P. to 4,000 B.P. (Terasmae, 1961: 666) when mean temperatures were about 6° F higher than at present. This was the " Hypsithermal " or " Climatic Optimum " period and its influence was widespread. It is quite certain that many species of plants and animals existed then well to the north of their present ranges. As the climate cooled, about 3,000 B.P., some of these species withdrew toward the south. Some populations appear to have survived in particularly favourable regions, e.g., in the Hudson Bay Lowland, and as neighbouring populations vanished these peripheral populations were isolated. There is reason to believe that the Hypsithermal Period played an important role in bringing about the present distribution patterns of many freshwater molluscs.

Existing Drainage Basin Connections

In addition to drainage basin confluences of the past, present connections between several adjacent drainage basins are also known to exist. These complicate the problems of origins and of immigration routes. The large Albany

River system in Ontario is joined to Lake Superior by Lake Nipigon and by Long Lake, both of which have north- and south-flowing outlets. The Rainy River-Winnipeg River system (Nelson River drainage) is also now connected with the Great Lakes-St. Lawrence River system at Saganaga Lake (48°15'N, 90°55'W, on the International Boundary), which drains both east and west. The Nelson and Churchill River systems are scheduled to be joined at Southern Indian Lake, Manitoba, in connection with a hydro-electric project. The Churchill and Mackenzie River systems are now connected at Wollaston Lake in northern Saskatchewan (58°15'N, 103° 20'W) which has 2 outlets.

Although some adjacent river systems appear to lack direct connecting links probably all those within and north of the boreal forest are partly separated from neighbouring systems only by muskeg. Muskeg serves as an eminently satisfactory habitat for many gastropods and sphaeriids, however, and is hardly a barrier to their passage. During periods of high water and perhaps at other times transmigration by fishes bearing unionid glochidia is clearly possible. Streams farther south may also be connected in times of high water or flood. Prior to the recent erection of dams the Red River (Nelson River drainage) and the Minnesota River (Mississippi-Missouri system) were periodically joined by floods (Dawley, 1947: 680). The Qu'Appelle River and the South Saskatchewan River must also have been occasionally so connected.

Even some marine waters are not necessarily a barrier to migrations between river mouths. In the summers of 1963 and 1965 I found that James Bay surface waters near the mouths of the Eastmain, Albany, and Attawapiskat rivers supported freshwater molluscs and were entirely fresh to the taste. During calm weather numbers of freshwater fishes and floating or vegetation-attached molluscs could easily drift along the coast from one river mouth to the next.

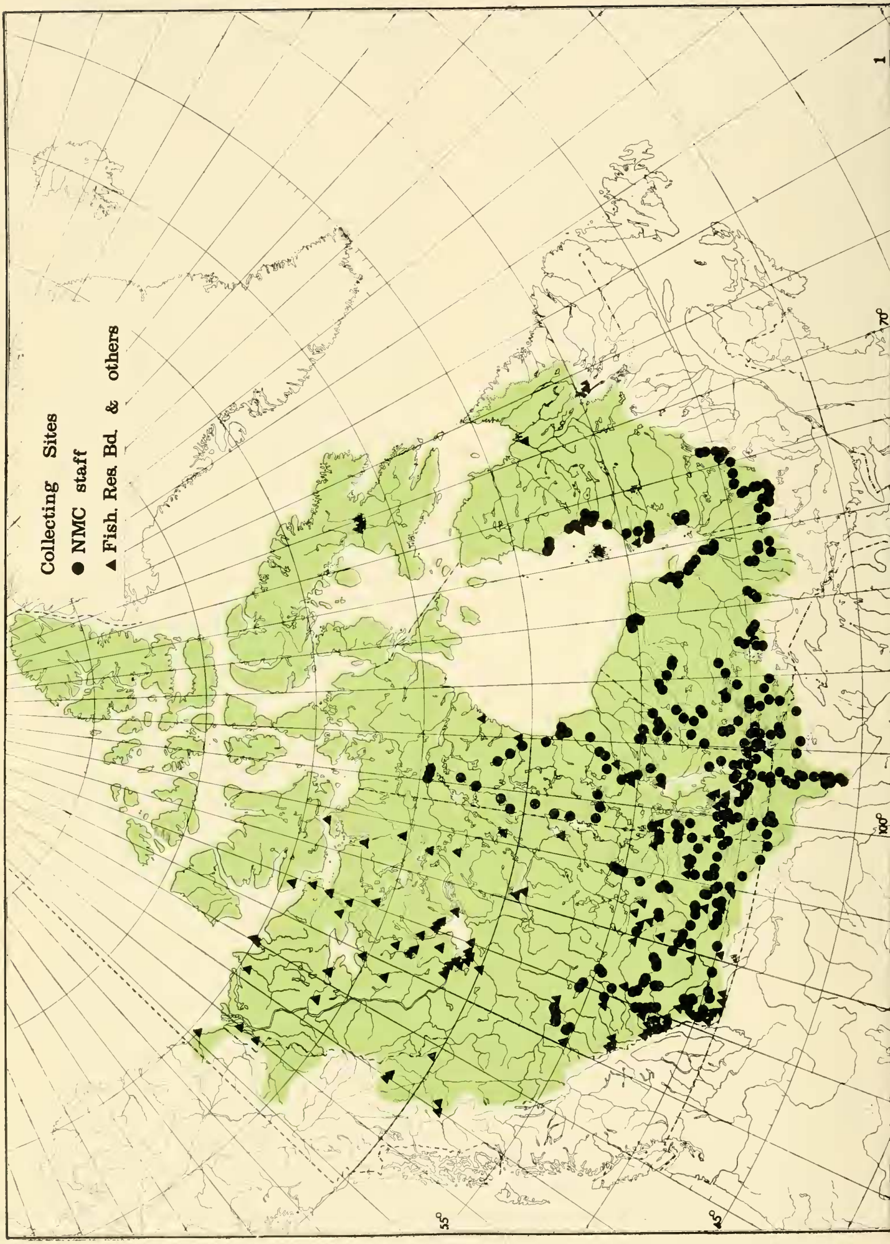
Vegetation and Climate

The Canadian Interior Basin transcends 6 phytogeographic regions (see back endpaper and Rowe, 1959).

The Arctic Region includes the northern part of the Ungava Peninsula, the Western Arctic Mainland north of an irregular boundary running from west-central Hudson Bay to the Mackenzie Delta, the Arctic Archipelago, the islands in Hudson Bay, and some mountainous areas of the Yukon Territory. Its southern border, the tree-line, corresponds well with the 50°F July mean-temperature isotherm. Vegetation is of the arctic tundra type and permafrost occurs throughout.

South of the tree-line is the great Boreal Forest Region. This forms a continuous belt from the Atlantic coast to the Rocky Mountains and Alaska and comprises the largest phytogeographic region in that part of the Canadian Interior Basin inhabited by molluscs. White and black spruce (*Picea glauca* and *P. mariana*) are the dominant trees and tamarack (*Larix laricina*), jack pine (*Pinus banksiana*), other conifers and a few broad-leaved trees are also abundant. In the northern part of the boreal forest the proportion of spruce and tamarack rises and the closed forest becomes an open lichen-woodland. This subarctic region is called the Transition Zone. The southern border of the Boreal Forest Region is approximataly concordant with the 65°F July mean-temperature isotherm.

The Grassland or Prairie Region extends across the southwestern part of the Canadian Interior Basin south of the boreal forest and through parts of Alberta, Saskatchewan, Manitoba, North Dakota, South Dakota, and Minnesota. A broad belt of mixed boreal forest and grassland,


Collecting Sites
● NMC staff
▲ Fish. Res. Bd. & others

the Western Parkland, lies along the northern boundary of this Region. Low annual rainfall is characteristic and several inland drainage basins exist there which have no outlets, e.g., the Quill Lakes and Old Wives Lake basins in Saskatchewan, Devil's Lake basin in North Dakota, and others.

Three other phytogeographic regions extend into the Canadian Interior Basin but do not occupy extensive areas there. The Great Lakes—St. Lawrence Forest Region occurs in the southern part of western Ontario and in adjacent parts of Minnesota. This region is characterized by a mixture of many coniferous and deciduous trees and pines, hemlocks, birches, maples, and oaks are common. The Subalpine Forest Region and the Montane Forest Region are both represented in the Rocky Mountains of Alberta. Endemic species of spruce, pine, and fir occur in each. Neither region extends sufficiently into the Canadian Interior Basin to constitute a significant component of its overall phytogeography, however.

Climatic regions within the Canadian Interior Basin parallel the phytogeographic regions. The subject is too broad and complex for detailed discussion here but some examples of temperature and precipitation averages follow. Resolute Bay on Cornwallis Island, an arctic community, has average temperatures of -20°F (maximum) and -33°F (minimum) in January and 45°F and 35°F in July. Mean annual precipitation there is 5·4 inches and mean annual snowfall is 29 inches. Daylight is continuous during the summer and is entirely absent for four months in winter. Moosonee, Ontario, a boreal community, has average temperatures of +5°F and −16°F in January and 71°F and 49°F in July. Total precipitation averages 31·0 inches and total snowfall 110 inches. Regina, Saskatchewan, a prairie city, has average temperatures of +11°F and −8°F in January, and 80°F and 53°F in July. The average total precipitation is 15·5 inches and total snowfall is 43 inches (data are from Thomas, 1967: 33).

Field Collecting and Field Data

Field work for this study began in October, 1959, with a short reconnaissance trip to the Cochrane area in northeastern Ontario in company with Dr. D. E. McAllister. An extensive collecting programme was begun in 1960 and was pursued annually until 1969. Supplementary collecting expeditions were also carried out by others, i.e., in 1961 by Mrs. Elizabeth Macpherson at Aberdeen Lake, N.W.T. (64°40′N, 100°00′W) and in 1965 by Mr. H. D. Athearn in the Prairie Provinces.

The distribution of all of these collecting stations has been plotted on Map 1. Complete station data are on file at the National Museum of Natural Sciences. An analysis showing the number of seasons during which each region was visited, relative collecting effort, and overall results is given in Table 1.

Distribution of collecting effort was determined by weather conditions, by accessibility, and by the regional distribution of material already received from other sources. About 600 supplementary lots were available, principally from the Northwest Territories and Alberta, and the total number of specimens studied from the Canadian Interior Basin is conservatively estimated at about 100,000.

Collecting techniques varied with the situation. A glass-bottomed viewing box was used for collecting mussels and large gastropods, a triangular dip-net was employed for sweeping mud and vegetation in shallow water for sphaeriids and gastropods, and a small dredge was used in deeper water. Where visibility was adequate, hand-picking was often the best method. Where it was poor

TABLE 1. Distribution of collecting effort and results.

Region	Field Seasons	No. of Stations	No. of Lots	Approx. No. of Specimens
Quebec	3	72	282	12,370
Ontario	9	191	1,249	26,280
Minnesota	2	13	82	2,220
North Dakota	2	18	116	1,590
Manitoba	7	103	708	15,310
Saskatchewan	3	87	413	10,680
Alberta	3	78	366	6,720
Northwest Terr.	3	15	57	5,340
Totals		577	3,223	80,510

because of turbidity (as in the Clay Belt) after the first collecting season a foam-rubber diving suit was worn for warmth and unionids were collected " by feel." Most specimens were first anaesthetized with nembutal and then preserved in 70% ethyl or 40% isopropyl alcohol in the field.

Most of the localities visited could be approached by road but many were more remote. Collecting near James Bay and Hudson Bay was done with canoes and the help of local guides. In 1963 localities between Inoucdjouac (Port Harrison), Quebec, and Poste de la Baleine (Great Whale River), Quebec, were visited by use of a Peterhead fishing boat manned by four Eskimos. During four seasons amphibious aircraft were chartered for investigation of remote lakes in Quebec, Ontario, Manitoba, and the Northwest Territories.

Field data recorded for each of the 577 survey collections are (1) station number, (2) precise location, (3) date, (4) collector or collectors, (5) time spent collecting, (6) method of capture, (7) nature and size of water body, (8) depths, (9) vegetation quality and abundance, (10) relative current speed (if any), (11) substrate quality, and (12) associated organisms and any additional observations made, e.g., water hardness, temperature, microhabitats, etc. These data were later transcribed on modified punch-cards. As the material was critically examined the identifications and quantities of specimens were also entered on the punch-cards. Retrieval of data on habitat-species associations, etc. was greatly facilitated by this method.

II. PRELIMINARY ANALYSIS AND CONCLUSIONS

Origins of the Fauna

Colonization of the Canadian Interior Basin by freshwater molluscs has undoubtedly been going on continuously

since the Wisconsin ice-sheet first began to recede from the land. Because of obvious faunal relationships, discussed below, it is reasonable to assume that the molluscs have come, and are coming, from 4 contiguous regions. These are the Alaska-Yukon (Beringian) Region, the Pacific and Rocky Mountain Region, the Mississippi-Missouri River drainage areas, and the Great Lakes-St. Lawrence River drainage area. Where necessary for brevity these will be called the Northwest, Southwest, South-Central, and Southeast regions, respectively. The first 3 were largely non-glaciated and the fourth, the Great Lakes-St. Lawrence River drainage area, was deglaciated and repopulated by molluscs before most of the adjacent parts of the Canadian Interior Basin became free of ice.

When distributions within and outside of the Canadian Interior Basin are examined one by one and possible migration routes are considered, the post-Wisconsin source area or areas of some species and subspecies appear to be clearly indicated. For example within the Canadian Interior Basin *Fusconaia flava* occurs only in the Red River and its tributaries. Outside of the Basin it occurs only in Lake Huron, Lake St. Clair, and Lake Erie and their tributaries and in the Mississippi-Missouri River drainage area immediately to the south of the Red River. Geological and other evidence shows that many opportunities have existed for direct faunal transmigration between the upper Mississippi River and upper Red River systems. Indirect transmigrations between the central Great Lakes and the Red River are also possible but these regions are more than 500 miles apart and *F. flava* occurs nowhere in the intervening area. It can be confidently assumed, therefore, that *F. flava* entered the Canadian Interior Basin from the Mississippi-Missouri River drainage area and only from that region.

The sources of other species are less apparent. For example *Sphaerium nitidum* is a cold-water species which has been found at many localities across the arctic part of the Canadian Interior Basin from Ungava to the Alaskan border, from northern Ontario to northern British Columbia, and in a few, isolated localities farther south (see Map 16). Outside of the Basin it occurs in Maine, throughout the Great Lakes, in the Rocky Mountains south to Utah, and from Washington to Alaska and the Aleutian Islands.

Since *Sphaerium nitidum* is abundant throughout a wide band of country extending through the Beringian Refugium and southeast inside the same climatic zone, it appears likely that it survived in the Beringian Refugium and was spread into other parts of Arctic and Subarctic Canada by passive transport. However, during Wisconsin glaciation a band of arctic or subarctic climate must also have existed close to the southernmost ice front. This might have provided suitable habitats for *S. nitidum* and the species might therefore also have invaded the Canadian Interior Basin from many sources in the south. The species is now rare or absent from southerly parts of the Canadian Interior Basin, however, so a plausible but rather less convincing case exists for southern regions acting as sources. Distributional evidence therefore points to Beringia with near certainty and indicates that the 2 southern areas are possible but uncertain.

Table 2 presents a summary of presumed post-Wisconsin source areas for all fresh water species and subspecies in the Canadian Interior Basin. Presumed source areas, based on present distribution patterns inside and outside of the Basin, are shown under " Origins " in the columns marked " P " (present). Source areas considered almost certain are shown by X, and those considered possible

TABLE 2. Summary of preliminary conclusions regarding (1) Post-Wisconsin origins of the fauna, (2) endemicity, (3) correlations of present distributions with isotherms for the July mean temperature, (4) correlations with geological regions, and (5) attainment of distributional equilibrium (see text). (Abbreviations: P=recent, F=fossil; C=relatively common to abundant, R=relatively rare to rare; for other symbols see text.)

	Origins									Isotherms							Geological Regions			
	North-west		South-west		South-central		South-east		Ende-micity								Interior Plain (IP)	Cana-dian Shield (CS)	Hudson Bay Low-land (HB)	Distrib. Equilib.
	P	F	P	F	P	F	P	F		40	45	50	55	60	65	65+				
UNIONIDAE																				
1. *Fusconaia flava*					X̲	(6)									—		C			—
2. *Quadrula quadrula*					X̲										—		C			—
3. *Amblema plicata*					X̲	(7)									—		C	R		—
4. *Elliptio complanata*							X̲							—	—			C	R	—
5. *Lasmigona costata*					X̲										—		R			—
6. *L. compressa*					X̲	(6)	X̲							—	—		C	R		—
7. *L. complanata*					X̲	(10)								—	—		C			+
8. *Anodonta grandis grandis*					X̲	(6)								—	—		C	C		+
9. *A. grandis simpsoniana*					x		x	(10)					—	—	—		C	C	C	+
10. *A. kennerlyi*			X̲											—	—		R			—
11. *Anodontoides ferussacianus*					X̲	(6)	X̲							—	—		C	R		—
12. *Strophitus undulatus*					X̲	(6)								—	—		C			—
13. *Proptera alata*					X̲										—		C			—

14. *Ligumia recta*				X	(7)									—	C			—
15. *Lampsilis*				X	(6)													
radiata					(10)	X						—	—	—	C	C	C	+
siliquoidea																		
16. *L. ovata*				X	(7)								—	—	C	R		—
SPHAERIIDAE																		
17. *Sphaerium*	X	(1)	x	x		x	(9)			—	—	—	—					
nitidium																		
18. *S. rhomboideum*	x		x	X		X	(8)					—	—	—	R	C	R	—
19. *S. simile*				X	(6)	X	(8) (9)					—	—	—	C	C	R	—
20. *S. striatinum*		(2)	X	X	(6)	X	(8)					—	—	—	C	C	C	—
21. *S. occidentale*				X		X							—	—		R	R	—
22. *S. lacustre*	X	(1 ?)																
		(4 ?)	X	X		X	(9)				—	—	—	—	C	C	C	+
23. *S. partumeium*				X		X							—	—	R	C		—
24. *S. securis*	x		X	X		X						—	—		R	C	R	—
25. *S. transversum*			x	X		X						—	—	—	C	R	R	—
26. *Pisidium*	X	(1)																
idahoense		(2–4)		x		X	(8)			—	—	—	—		R	C	R	—
27. *P. adamsi*				x		X	(8)				—	—	—	—		C	R	—
28. *P. casertanum*	X	(1)	X	X		X	(8)											
		(2–5)					(9)		—	—	—	—	—	—	C	C	C	+
29. *P. compressum*	x		X	X		X	(8)											
							(9)				—	—	—	—	C	C	C	+
30. *P. equilaterale*						X							—	—		R		—
31. *P. fallax*				X		X	(8)					—	—	—	R	R	R	—
32. *P. ferrugineum*	X	(4, 5)	X	X		X	(9)			—	—	—	—	—	C	C	R	+
33. *P. lilljeborgi*	X	(1)	X	X		X	(8)		—	—	—	—	—	—	C	C	C	+
		(2–5)																
34. *P. milium*	X	(1)	X	X		X						—	—	—	C	C	R	—
		(4)																
35. *P. nitidum*	X	(1)	X	X	(6)	X	(8)			—	—	—	—	—	C	C	C	+
		(4, 5)																
36. *P. subtruncatum*	X		X	X		X	(8)			—	—	—	—	—	C	C	C	—
37. *P. variable*	x		X	X		X	(8)				—	—	—	—	C	C	C	+

TABLE 2—(*Contd.*)

	Origins									Isotherms							Geological Regions			
	North-west		South-west		South-central		South-east		Endemicity								Interior Plain (IP)	Canadian Shield (CS)	Hudson Bay Lowland (HB)	Distrib. Equilib.
	P	F	P	F	P	F	P	F		40	45	50	55	60	65	65+				
38. *P. ventricosum*	x	(1) (4,5)	X		X		X				—	—	—	—	—		C	C	C	+
39. *P. walkeri*		(4)			X		X					—	—	—	—		C	C	C	—
40. *P. conventus*	X		X		X		X	(8)			—	—	—	—			R	C	R	—
41. *P. punctatum*					X		X						—	—	—		R	R	R	—
VIVIPARIDAE																				
42. *Campeloma decisum*					X										—		C	C		—
VALVATIDAE																				
43. *Valvata sincera sincera*					X		X					—	—	—	—		R	C	R	—
44. *V. sincera ontariensis*									X					—	—			C		—
45. *V. sincera helicoidea*	X	(1) (2, 5)	X		X	(6)	X				—	—	—	—			C	C	C	+
46. *V. tricarinata*	x		x		X	(6)	X	(8) (9)				—	—	—	—		C	C	C	—
HYDROBIIDAE																				
47. *Cincinnatia cincinnatiensis*					X										—		C			—
48. *Marstonia decepta*					X		X	(8) (9)						—	—			C		—
49. *Probythinella lacustris*	X				X		X	(8)					—	—	—		C	C	C	—

50. *Amnicola walkeri*			X	X			C	R	—
51. *A. limosa*		(2)	X	(6) X (8) (9)		C	C	C	—
ACROLOXIDAE									
52. *Acroloxus coloradensis*		X		X		R	R		—
LYMNAEIDAE									
53. *Lymnaea decampi*	x		X	X (9)		C	C	R	—
54. *L. exigua*				X		R	R	C	—
55. *L. modicella*	x	X	X	X		C	R	R	—
56. *L. parva*		(4, 5) X	X	X		C	C	C	—
57. *L. bulimoides*		X	X			C			+
58. *L. dalli*		X	X			R			+
59. *L. columella*			X			R			—
60. *L. megasoma*			X	X		C	R		—
61. *L. stagnalis appressa*	x	(1) X	X	X (8)		C	C	C	—
62. *L. stagnalis sanctaemariae*				X			R		—
63. *L. atkaensis*	X	(1)				R			—
64. *L. caperata*		X	X			C	R		—
65. *L. montanensis*		X				R			—
66. *L. arctica*	X					C	C	C	+
67. *L. kennicotti*	x	(4)				R	R		—
68. *L. catascopium catascopium*	x	X	X	X		C	C	C	+
69. *L. catascopium nasoni*				X			R		—
70. *L. catascopium preblei*					X		R		—
71. *L. elodes*	X	(1) X	X	X		C	R	R	+

TABLE 2—(*Contd.*)

	Origins									Isotherms	Geological Regions			
	North-west		South-west		South-central		South-east		Ende-micity		Interior Plain (IP)	Cana-dian Shield (CS)	Hudson Bay Low-land (HB)	Distrib. Equilib.
	P	F	P	F	P	F	P	F		40 45 50 55 60 65 65+				
72. *L. proxima*	x		X̲								C			—
73. *L. reflexa*			X̲		X̲		X̲				R	R		—
PHYSIDAE														
74. *Physa jennessi jennessi*	X̲	(1) (4)									C	C	C	+
75. *P. jennessi athearni*									X̲		R			—
76. *P. jennessi skinneri*	x		X̲		X̲		X̲				C	R	C	—
77. *P. gyrina*	x		X̲		X̲		X̲	(9)			C	C	C	—
78. *P. johnsoni*									X̲		R			—
79. *Aplexa hypnorum*	X̲		X̲		X̲		X̲				C	R	C	—
PLANORBIDAE														
80. *Gyraulus deflectus*	x		X̲		X̲		X̲				C	C	C	+
81. *G. circumstriatus*	x	(1)	X̲		X̲		X̲				C			+
82. *G. parvus*	x	(1)												
		(4?, 5)	X̲		X̲	(6)	X̲	(9)			C	C	C	+
83. *Armiger crista*		(1)	X̲		X̲	(6)	X̲				C		R	—
84. *Promenetus exacuous exacuous*	X̲		X̲	(4)	X̲		X̲				C	C	C	+
85. *P. exacuous megas*			X̲		X̲						C			+

86. *P. umbilicatellus*		X	X								—	—		C			+
87. *Menetus cooperi*		X									—	—		R			—
88. *Planorbula armigera*	x	X	X	X						—	—	—		C	C	C	—
89. *P. campestris*		X	X								—	—		C			+
90. *Helisoma anceps anceps*		X	X	(6) X (8) (9)					—	—	—	—		C	C	C	—
91. *H. anceps royalense*				X							—	—			C		—
92. *H. campanulatum campanulatum*			X	X					—	—	—	—			C	R	—
93. *H. campanulatum collinsi*					X						—	—			C		—
94. *H. trivolvis trivolvis*				X						—	—	—			C	C	—
95. *H. trivolvis subcrenatum*	x	(1) X	X							—	—	—		C	R		+
96. *H. pilsbryi infracarinatum*			X	X							—	—		C	C		+
97. *H. binneyi*		X									—	—		R			—
98. *H. corpuleuntum corpulentum*			X	X							—	—			C		—
99. *H. corpulentum vermilionense*					X							—			R		—
100. *H. corpulentum whiteavesi*					X							—			R		—
ANCYLIDAE																	
101. *Laevapex fuscus*				X							—	—			R		—
102. *Ferrissia rivularis*			X	X						—	—	—		C		C	—
103. *F. parallela*			X	X							—	—		R	C		—

but rather doubtful are indicated there by *x*. Fortunately, fossil evidence exists which supplements many of these tentative decisions. Relevant published and unpublished evidence known to me is cited by index number in Table 2 under " Origins " in the columns marked " F " (fossil). The index numbers refer to the references below.

(1) McCulloch, Taylor & Rubin, 1965. Kotzebue Sound area, Alaska; 24 samples reported ranging in age from Illinoian to Recent. Data referred to in Table 2 are of Wisconsin (34,000±200 B.P. to >38,000 B.P.) and late Wisconsin to early Recent (7,270±350 B.P. to 11,340 ±400 B.P.) age.

(2-5) Wisconsin Stage to early Recent shells collected in Yukon Territory by C. R. Harington, 1967. The Sphaeriidae were identified by H. B. Herrington and the gastropods by A. H. Clarke. The ostracods from these sites have been described by Delorme (1968).

(2) Bank of Old Crow River, 3 localities between 67°52′N, 139°48′W and 68°13′N, 140°00′W, estimated age 38,000–40,000 B.P.

(3) Bank of Old Crow River, same area, estimated age 22,000 B.P.

(4) Bank of Porcupine River, 67°33′N, 138°53′W, estimated age slightly over 10,000 B.P.

(5) Near Mayo Airport, Mayo, Y.T., possibly early post-glacial.

(6) Tuthill, 1967. Wisconsin Stage and post-hypsithermal molluscs of Lake Agassiz deposits in North Dakota and Minnesota.

(7) Dawley, 1947. Lake Agassiz molluscs from Minnesota.

(8) Zoltai, and Herrington 1966. Late Wisconsin and early Recent (5,130 to >9,380 B.P.) molluscs from north of Lake Superior.

(9) Clowers, 1966. Late Wisconsin (*ca.* 8,000 to 9,500 B.P.) molluscs from eastern Ontario (5 sites).

(10) Post-Pleistocene shells of *Anodonta grandis simpsoniana* from Lake Algonquin, precursor of Lake Huron. See under *A. g. simpsoniana*, this work.

Several conclusions may be drawn from an examination of Table 2 as follows:

(1) Of the 199 " virtually certain " positive relationships proposed between species or subspecies and source areas, 56 (28%) are supported by fossil evidence. Of the 31 " possible " positive relationships proposed, 9 (29%) are also supported by fossil evidence. Of the 183 negative relationships proposed (i.e. where a region was considered not to be a source area) 5 (2·7%) were contradicted by fossil evidence. To put it another way, 93%, or 65 of the 70 species and subspecies known as Wisconsin or post-Wisconsin fossils from relevant areas, contribute substantiating evidence for relationships proposed on the basis of present distributions. The fossils also indicate that present distributions provide a good, but not entirely reliable, basis for conclusions about faunal origins.

(2) Fossil evidence indicated that 2 species, *Sphaerium striatinum* and *Amnicola limosa*, occurred in Beringia about 38,000 to 40,000 B.P. From consideration of present distributions Beringia would not have been expected as a post-Wisconsin source area for these species. It is possible, however, that *S. striatinum* and *A. limosa* did not persist in Beringia but became extinct there prior to Recent time.

(3) Fossil evidence also indicates that in contradiction to expectations 3 other species, *Pisidium walkeri*, *Lymnaea parva*, and *Armiger crista*, existed in Beringia during late Wisconsin or early Recent time. All these are inconspicuous and their apparent current absence from nearby areas may be due to insufficient collecting.

(4) The approximate relative contributions of each of the 4 source regions to the total fauna of the Canadian Interior Basin may be easily calculated if, for the purposes of calculation, all source regions for which *any* " positive " Recent or fossil evidence exists are considered " positive " and all others are considered " negative ". The results are given in Table 3.

TABLE 3. Approximate number of species and subspecies contributed by each source region to the fauna of freshwater molluscs of the Canadian Interior Basin. (See text.)

Region	Species and Subspecies	%
Beringian	42	17·4
Pacific—Rocky Mountain	49	20·2
Mississippi—Missouri rivers	78	32·2
Great Lakes—St. Lawrence River	66	27·2
Autochthonous Endemics	7	2·9
Cumulative Totals	242	99·9

(5) The 7 species and subspecies which occur only within the Canadian Interior Basin are *Valvata sincera ontariensis*, *Lymnaea catascopium preblei*, *Physa jennessi athearni*, *P. johnsoni*, *Helisoma campanulatum collinsi*, *H. corpulentum vermilionense*, and *H. corpulentum whiteavesi*. Since no contradictory information is available, these are here considered as autochthonous endemics. Four of these taxa are distributed near the Lake Superior region, an area implicated as an important centre for speciation in boreal North America (Clarke, 1970b).

Correlations with Temperature and Geology; Distributional Equilibrium

Table 2 presents correlations, based on available information derived from this study, of species and subspecies distribution both in relation to isotherms of July mean temperatures and to 3 main geological regions within the Canadian Interior Basin, i.e., the Interior Plains (this includes the edge of the Cordilleran Region and is abbreviated as IP), the Canadian Shield (abbreviated CS) and the Hudson Bay Lowlands (HB).

Although water temperatures, especially *in situ*, are more meaningful than air temperatures, such information is not available. Isotherm locations as published are also not precise. It appears likely that correlation of distributions with isotherms of air temperatures, when refined, will be useful for interpreting palaeoclimates from fossil molluscan assemblages although, as pointed out by Taylor (1965), the ecologies of Recent and Pleistocene populations of the same species are not necessarily identical. Nevertheless, presentation of the information which is now available is considered worthwhile even though it is certain to be rather inaccurate.

Fifteen species and subspecies exist close to or north of the isotherm of the July mean temperature of 45°F and thereby exhibit maximal cold-tolerance. This temperature appears to be close to the lowest July mean temperature that is consistent with perpetuation of freshwater mollusc populations. These species and subspecies are *Sphaerium nitidum*, *Pisidium idahoense*, *P. casertanum*, *P. ferrugineum*, *P. lilljeborgi*, *P. nitidum*, *P. subtruncatum*, *P. ventricosum*, *P. conventus*, *Valvata*

sincera helicoidea, *Lymnaea atkaensis*, *L. arctica*, *L. kennicotti*, *Physa jennessi jennessi*, and *Aplexa hypnorum*. The distributions of these species and subspecies also extend toward the south for varying distances and cross other isotherms. The correlations with the highest mean July temperatures found for these molluscs are about 55° for *Lymnaea kennicotti*, 58° for *Physa jennessi jennessi*, 60° for *Lymnaea atkaensis* and *L. arctica*, and higher values for all others. One of these species, *Pisidium casertanum*, must have summer and winter temperature tolerance limits which are very broad. This species is apparently world-wide and is the only freshwater mollusc known that is so widely distributed.

Proceeding southward across other July mean-temperature isotherms the number of species increases markedly, as follows: 45°, 15 species and subspecies; 50°, 29; 55°, 47; 60°, 65; and 65°, 96. It is quite clear that virtually all species within the Canadian Interior Basin reach their limits of both summer and winter cold-tolerance there. Further studies which seek to determine these limits more precisely might well be concerned with populations from that Basin.

Geological correlations shown in Table 2 were arranged to assess the relative effects of calcium abundance in the Interior Plains (IP) and the Hudson Bay Lowland (HB) and calcium scarcity in the Canadian Shield (CS). (C indicates that the species or subspecies is relatively common to abundant and R indicates that it is relatively rare to rare.)

In summary, 85 species and subspecies occur in the Interior Plains, 77 occur in the Canadian Shield, and 53 occur in the Hudson Bay Lowlands. A total of 45 species and subspecies occur in all 3 regions, 23 occur in 2 regions (IP and CS, 15; CS and HB, 6; IP and HB, 2), 23 occur only in the Interior Plains, 12 occur only in the Canadian Shield, and none are restricted to the Hudson Bay Lowland.

Of the 68 species and subspecies, which are known from both the Interior Plains and the Canadian Shield (i.e., IP, CS, and HB or IP and CS), 42 are classed either as C in both regions or as R in both regions and 26 are classed as C in 1 region and R in the other. Of these 26, 13 are classed as C in IP and R in CS and 13 others are classed as R in IP and C in CS. Of the 51 which occur in both the Canadian Shield and the Hudson Bay Lowland (i.e., IP, CS, and HB or CS and HB), 35 are classed either as C in both regions or as R in both regions and 16 are classed as C in one region and R in the other. Of these 16, 13 are classed as C in CS and R in HB and 3 are classed as R in CS and C in HB.

These results show that the total faunal differences between the Interior Plains and the Canadian Shield are not as great as one would predict from impressions gained in the field. The Unionidae account for the most obvious differences, since all the thick shelled and highly sculptured species or half of the total number of unionids occur only in the Interior Plains. There is also a marked decrease in the number of species and subspecies inhabiting the Hudson Bay Lowland when compared with the Canadian Shield. Impressions of relative richness in the Lowlands are also misleading and are caused by the greater abundance of individuals but not actually by an increase in numbers of species.

Apparently the Interior Plains were populated chiefly by calciphile species from the lime-rich south-central region. The Canadian Shield was populated principally by species with tolerances for low concentrations of calcium and were partly derived from lime-poor southeastern areas. Neither group appears to hold a selective advantage when later

migrating into the other's territory. Species now in the Hudson Bay Lowland, with some exceptions, have had to migrate across the Shield. The Canadian Shield has functioned as a filter-bridge and some species and subspecies appear either to have reached their low temperature tolerance limits during the passage or to have been halted by other factors. Many of those which completed the migration appear to have thrived in the Hudson Bay Lowland.

The final column in Table 2 shows the species that are here considered to have nearly or completely attained distributional equilibrium (indicated by +) within the Canadian Interior Basin and those which have not (indicated by —). These conclusions have been reached by comparing the distributions of the molluscs within the Basin with isotherms, rainfall, phytogeographic regions, bedrock geology, Pleistocene geology, and, where appropriate, with the distributions of the same species outside of the Canadian Interior Basin.

Based on these criteria only 27 of the 103 species and subspecies here treated are judged to populate now most or all of the region in which they are capable of growth and reproduction. These 27 are presumed to have reached distributional equilibrium. This is interpreted to mean that these species and subspecies appear now to be geographically more stable than the other 76 and to occupy ranges which are less likely to become significantly altered in size in the near future. For example, 22 of the 76 species and subspecies whose ranges are considered relatively unstable are absent from the Canadian Shield east of Hudson Bay and James Bay although their distributions elsewhere on the Shield indicate that they could probably live in much of that eastern region.

Other limiting factors may well exist which are not yet understood and the estimate of species and subspecies not at distributional equilibrium may be too high. But even if this is so, the number whose distributional limits are relatively dynamic is remarkably great and well in keeping with the youthfulness of the environment.

III. SYSTEMATICS

Explanation

On the following pages the freshwater molluscan fauna of the Canadian Interior Basin is discussed at all taxonomic levels. Although the arrangement of the text is meant to be straightforward, a short statement regarding synonymies, measurements, and some other subject headings is desirable.

Synonymies. These are limited to (a) those names which are of present significance in matters of priority and (b) synonyms which have been used erroneously in recent publications (prior to 1969) as valid names. Names which have been recognized for many years as junior synonyms are not repeated but references containing extensive synonymies are cited.

Descriptions, Illustrations, and Keys. These are based on specimens from the Canadian Interior Basin except where otherwise indicated.

Distribution Maps. The green areas shown on the maps define the Canadian Interior Basin and only localities which are within that area have been designated by spots on the maps. In most cases this does not represent the total range of the mollusc being discussed. Total ranges are given under " Distribution ".

Measurements. These refer to randomly collected population samples. Their statistical reliability is limited only by the size of the sample and by possible, though inadvertent, bias inherent in collecting procedures. Large lots were ran-

domly subsampled and smaller lots were measured in their entirety except where otherwise indicated. In calculations of standard deviation (S.D.) and standard error of the mean ($S.E._{M}$) N-1 was used where N was 15 or less. Morphological features and standard character measurements (length, height, etc.) are defined in Text Figures 1 to 3 and 5 to 9. Other character measurements are defined in the text.

Records. Specimens examined are cited by date collected followed by collector's name and an exclamation mark. To avoid confusion, literature references are cited by author followed by date and page. All references cited under Records or elsewhere in the text are included in full in the bibliography. Distances given in miles refer to highway mileage measured from the centre of a city, town, or village, wherever possible and unless otherwise specified. In areas without roads (Northern Ontario, most of the Northwest Territories, etc.) these distances refer to airline miles. Locations of all municipal centres and geographical features mentioned are given in the Gazetteers of Canada published by the Canadian Permanent Committee on Geographical Names and available from the Queen's Printer, Ottawa. See also the front end-paper map.

Abbreviations. In addition to abbreviations defined in the text, the following abbreviations are used for names of institutions:

AMNH	American Museum of Natural History, New York, New York
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania.
Fish. Res. Bd.	Fisheries Reseach Board, Canada Department of Fisheries and Forestry, Ottawa.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
NMC	National Museums of Canada, National Museum of Natural Sciences, Ottawa.
UMMZ	University Museums, Museum of Zoology, University of Michigan, Ann Arbor, Michigan.
USNM	United States National Museum, Washington, D.C.

Technical terms. The morphological terms not defined in the text figures are standard in the malacological literature. A convenient glossary of these terms has been published by R. C. Moore, 1960, *Treatise on Invertebrate Paleontology, Part I* (*Mollusca* 1), p 129–134. See also Fretter & Graham (1962).

Phylum Mollusca

Molluscs are soft-bodied invertebrate animals characterized by the possession of (1) a well-developed anterior head (absent in Pelecypoda) with tentacles, eyes, mouth, and radula; (2) a ventral, muscular foot used for crawling, burrowing, and attachment; (3) a dorsal visceral mass containing most of the internal organs; and (4) an enveloping sheet of tissue, the mantle, which in most species secretes a calcareous shell. The mantle cavity is the respiratory chamber and initial receptor for food particles (in filter-feeding groups) and for reproductive and excretory products. Clams, mussels, oysters, snails, slugs, chitons, squids, and octopuses are molluscs. For thorough definitions and descriptions of the Phylum Mollusca and its Classes see Yonge (1960) and Morton & Yonge (1964).

The Mollusca are known from Cambrian to Recent deposits and constitute one of the most ancient of animal groups. The Phylum contains between 50,000 and 100,000 living species and subspecies (opinions differ) and is second only to the Arthropoda (insects, crustaceans, spiders, etc.) in size. Molluscs live in the sea, in fresh water, and on the land.

Six Classes of Mollusca are recognized:

1. Monoplacophora. Six living species of Monoplacophora have been described, all from the deep-sea benthic epifauna and all members of a single genus, *Neopilina*. They are bilaterally symmetrical, partly segmented internally, with 5 or 6 pairs of gills surrounding the foot, an anterior mouth, a posterior anus, and a limpet-like shell. Monoplacophora are an archaic (Cambrian to Recent) and primitive group presumably similar to the ancient ancestors of all Mollusca. See Lemche & Wingstrand (1959) for details.

2. Amphineura. Chitons (Polyplacophora) and solenogastres (Aplacophora), marine, epifaunal, world-wide, and living from intertidal to abyssal depths. Considered as 2 classes by some anthors.

3. Scaphopoda. Tooth or tusk shells, marine, infaunal, world-wide, and found from subtidal to abyssal depths.

4. Pelecypoda. Clams, mussels, oysters, scallops, etc.; epifaunal and infaunal; marine and freshwater; and comprising about 30% of all Mollusca.

5. Gastropoda. Snails and slugs; epifaunal and infaunal; marine, freshwater, and terrestrial; and comprising about 65% of all Mollusca.

6. Cephalopoda. Squids and octopuses, marine, free-swimming (squids) and benthic epifaunal (most octopuses), world-wide, and living from subtidal to abyssal depths.

Key to the families of freshwater Mollusca found in the Canadian Interior Basin

1. Shell bivalved (Pelecypoda) 2
   Shell univalved, i.e., spiral or cap-shaped (Gastropoda) 3
2. Shell large, length more than 25 mm, lateral teeth, if present, posterior to the pseudocardinal teeth . . . . . . Family UNIONIDAE (p 26)
   Shell small, length less than 25 mm, lateral teeth present both anterior and posterior to the pseudocardinal teeth . . . . Family SPHAERIIDAE (p 131)
3. Operculum present (Prosobranchia) 4
   Operculum absent (Pulmonata) 6
4. Shell more than 10 mm high, living adults containing shelled juveniles within . . . . Family VIVIPARIDAE (p 215)
   Shell less than 10 mm high, living adults containing no juveniles within 5
5. Operculum circular and multispiral, aperture circular . . . . . Family VALVATIDAE (p 221)
   Operculum ovate or auriform and paucispiral, aperture ovate . . . . Family HYDROBIIDAE (p 240)
6. Shell spiral. 7
   Shell limpet-like (i.e., saucer-shaped or cap-shaped) 9
7. Shell conispiral and dextral (i e., with elevated spire coiled in a clockwise direction when viewed from above) . . . . Family LYMNAEIDAE (p 265)
   Shell not as above 8
8. Shell conispiral and sinistral (i.e., with elevated spire coiled counter-clockwise when viewed from above) . . . . Family PHYSIDAE (p 361)
   Shell planispiral (i.e., coiled in a flat plane) and dextral or sinistral . . . . Family PLANORBIDAE (p 388)
9. Apex pointed, acute, and located posteriorly and to the left. Very rare . . . . Family ACROLOXIDAE (p 261)
   Apex blunt and located posteriorly and either in the mid-line or to the right. Common . . . . Family ANCYLIDAE (p 473)

Class Pelecypoda

The Class Pelecypoda (synonyms: Lamellibranchia and Bivalvia) contains approximately 200 living and extinct families (Vokes, 1967). Almost all species possess calcareous bivalved shells joined together at the dorsal margin by a horny ligament. A few parasitic genera have lost their shells and some marine groups (e.g., Pholadidae, Teredinidae) bear accessory plates and other calcified structures. The head is absent and no radula, tentacles, or eyes are present although tactile-sensitive mantle projections (e.g., in Unionidae and Limidae) and light-sensitive mantle areas (e.g., Unionidae and Pectinidae) may be developed. In most families the foot is adapted for digging. Feeding is accomplished chiefly by filtering particles from the surrounding water. Fertilization is internal or external and in most species the sexes are separate. Bivalves occur only in marine and freshwater habitats; there are no terrestrial species.

Several systems for subdividing the Pelecypoda are in use based on hinge structure, musculature, and other anatomical features (e.g., see Thiele, 1935; Keen,

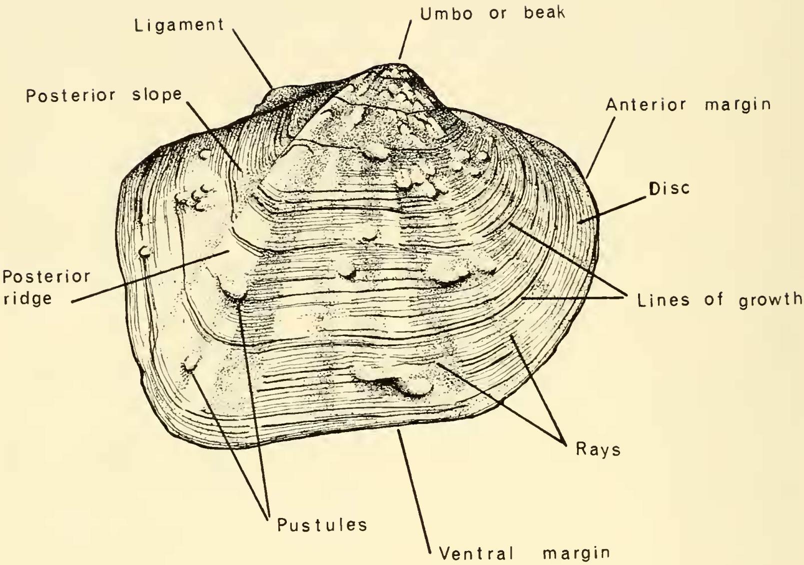


FIG. 1. Exterior morphology of a freshwater mussel shell (right valve of *Quadrula quadrula*, semi-diagrammatic).

1963; and Vokes, 1967). There is no agreement. The system used in this work is therefore conservative and recognizes 5 orders, viz., Protobranchia, Filibranchia, Anisomyaria, Eulamellibranchia, and Septibranchia (see Clarke, 1962). Only the Eulamellibranchia are well represented in freshwater and an species in the Canadian Interior Basill are members of that order.

Order Eulamellibranchia

Eulamellibranchia are characterized by (1) a heterodont hinge containing a few hinge teeth of diverse shape and size; (2) dimyarian musculature, i.e., with 2 adductor muscles of about the same size, 1 anterior and 1 posterior; (3) the mantle partly or completely closed and in most families with siphons well-developed; and

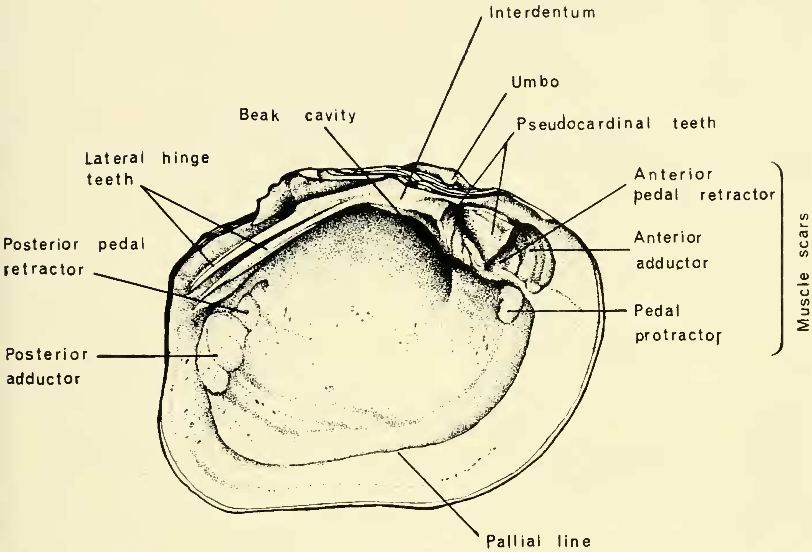


FIG. 2. Interior morphology of a freshwater mussel shell (left valve of *Quadrula quadrula*).

(4) leaf-like gills or ctenidia within the mantle cavity. This is the largest order of pelecypods and contains both marine and freshwater representatives.

Superfamily Unionacea

Unionacea are dimyarian heterodont freshwater bivalves with nacreous shells whose larva is a glochidium, i.e., a larva with an enveloping subcircular bivalved shell with or without marginal hooks, and adapted for temporary obligatory attachment to certain species of fishes (in nearly all cases) during which metamorphosis necessary for further development and growth takes place. Dispersal occurs during this parasitic stage.

The Superfamily Unionacea contains 3 families, viz., Margaritiferidae, Unionidae, and Hyriidae (see Parodiz & Bonetto, 1963). These are characterized by internal

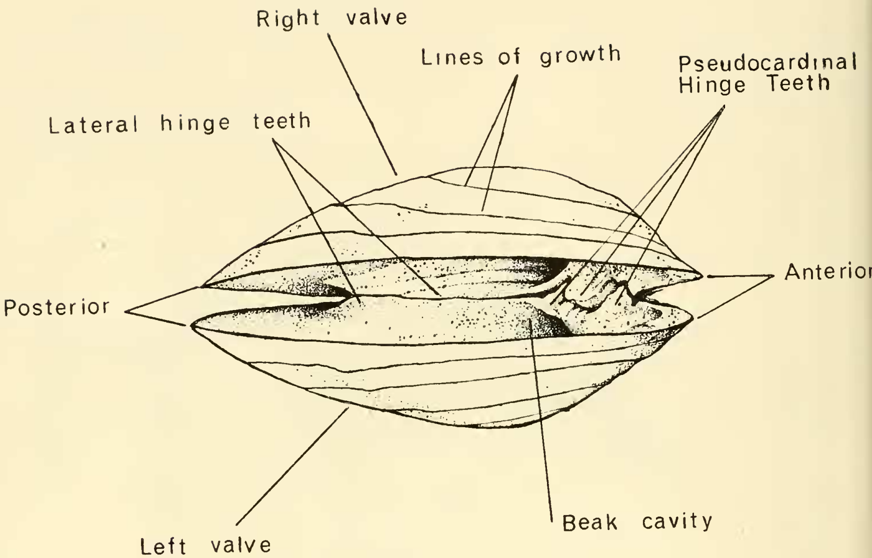


FIG. 3. Interior view of a gaping freshwater mussel shell showing articulation of hinge teeth (*Lampsilis ovata*).

anatomy and beak sculpture. Only the Unionidae occur in the Canadian Interior Basin.

Family UNIONIDAE Fleming

Unionidae Fleming, 1828: *A History of British Animals*, p 408, 415. Type Genus: *Unio* Philipsson, 1788. This family name has been placed on the Official List of Family-Group Names in Zoology by the International Commission on Zoological Nomenclature (Opinion 495).

Shells small to large (1 to 8 inches long or more); nacreous; variously sculptured; and with or without anterio-dorsal pseudocardinal and posterio-dorsal lateral hinge teeth. Beak sculpture variable but basically concentric. Dioecious (most) and larviparous (all). The glochidium larva in nearly all species is parasitic on fishes for a few days or weeks after emergence from the parental marsupium. All Unionidae are phytophagous filter-feeders.

This is a large, complex, and world-wide family occurring principally in the Northern Hemisphere. The Ohio-Mississippi River system and the Gulf of Mexico drainage area are particularly rich in species. Geologic range: Triassic to Recent.

The most important works on Unionidae published during this century prior to 1969 are by Simpson (1900, 1914), Ortmann (1911, 1919), Frierson (1927),

and Baker (1928b). Other significant contributions are cited in the text below.

Key to Species and Subspecies of Unionidae

1. Articulating hinge teeth absent or vestigial 2
   Articulating hinge teeth present 6
2. Vestigial pseudocardinal teeth indicated by a more or less prominent depression and thickening just anterior to the beak. Nacre commonly with salmon or pink suffusions near the beak cavity . . . . *Strophitus undulatus* (p 95, Pl. 6, Figs. 7, 8).
   Pseudocardinal teeth entirely absent 3
3. Ridges of beak sculpture single-looped and oblique, i.e., not parallel with concentric lines of growth. Length approximately 75 mm or less . . . . *Anodontoides ferussacianus* (p 92, Pl. 6, Figs. 5, 6).
   Ridges of beak sculpture double-looped or, if single-looped, not oblique. Length exceeding 75 mm in most specimens . . . 4
4. Beak sculpture distinctly double-looped, lower apices of loops elevated and nodulous, forming 2 short radial rows of nodules on each valve. Southern and western Canadian Interior Basin only . . . . *Anodonta grandis grandis* (p 81, Pl. 5, Figs. 1–4).
   Beak sculpture single-looped or slightly double-looped, but not nodulous 5
5. Beak sculpture ridges 4 to 6. Northern and eastern Canadian Interior Basin...*Anodonta grandis simpsoniana* (p 85, Pl. 5, Figs.5–10).
   Beak sculpture ridges 7 to 10. Western Alberta and British Columbia . . . . *Anodonta kennerlyi* (p 90, Pl. 6, Figs. 1–4).
6. Shell thick, relatively short (height/length> 0.65), and with prominent, wide ridges or tubercles on the disc 7
   Shell not as above 8
7. Disc area of each valve traversed by 2 wide, divergent ridges, which originate at the umbones and which, near the centre of each valve, are approximately perpendicular to the lines of growth. Ridges normally bearing numerous, prominent, elevated tubercles. Periostracum brownish to yellowish-green and with or without rays . . . . *Quadrula quadrula* (p 32, Pl. 1, Figs. 3, 4).
   Disc area of each valve traversed by 3 or 4 wide, nearly parallel ridges, which originate on the anterior part of the disc and which, near the centre of each valve, cross the lines of growth at an oblique angle (50° to 60°). Ridges normally quite smooth or with wide, flattened swellings only. Periostracum blackish to brownish and without rays . . . . *Amblema plicata* (p 35, Pl. 1, Figs. 5, 6; Pl. 2, Figs. 1, 2).
8. Shell triangular-ovate, heavy, and with thick and heavy hinge teeth. Length approximately 100 mm or less. Height/length> 0.70. Posterior pointed basally. Periostracum without rays . . . . *Fusconaia flava* (p 28, Pl. 1, Figs. 1, 2).
   Shell not as above 9
9. Shell with rounded, nearly parallel ridges on the posterior slope perpendicular to the lines of growth. Ridges well-developed to partly obscure. Interdental projection prominent. Height/length<0.60 . . . . . . *Lasmigona costata* (p 41, Pl. 4, Figs. 3, 4).
   Shell not as above 10
10. Interdental projection in left valve present and articulating with interdental depression in right valve. Nacre not purple 11
    Interdental projection not present 12
11. Shell large (adults approximately 90 mm in length, or more) and with a dorsal wing. Height/length>0.60 . . . . *Lasmigona complanata* (p46, Pl. 4, Figs. 5, 6).
    Shell medium-sized (adults less than 90 mm in length) and without a dorsal wing, except in juvenile specimens. Height/length<0.60 *Lasmigona compressa* (p 44, Pl. 4, Figs. 1, 2).
12. Shell large (adults approximately 90 mm in length or more) and with a dorsal wing. Height/length>0.60 13
    Shell without a dorsal wing 14
13. Nacre purple or pink. Lateral hinge teeth long and well-developed . . . . *Proptera alata* (p 99, Pl. 7, Figs. 1, 2).
    Nacre white. Lateral hinge teeth short and poorly developed or absent . . . *Lasmigona complanata* (p 46, Pl. 4, Figs. 5, 6).
14. Shell elongate (height/length<0.50), rounded or centrally pointed posteriorly, commonly exceeding 100 mm in length, and sexually dimorphic. Nacre white to purple . . . . *Ligumia recta* (p 102, Pl. 8, Figs. 1–4).
    Shell not so elongate (height/length>0.50) and not as above 15
15. Shell variable, subrhomboid, posterior obliquely subtruncate. Posterior ridge well-marked. Periostracum of most specimens dark and rayless. Nacre purple white, or orang . Beak sculpture single-looped.

Sexual dimorphism not apparent . . . . . *Elliptio complanata* (p 38, Pl. 3, Figs. 1–6).

Shell subelliptic to subovate. Posterior ridge obsolete. Periostracum in most specimens prominently rayed. Nacre normally white. Beak sculpture double-looped. Sexual dimorphism apparent 16

16. Shell ovate and relatively high. Height/length in males 0.60 to 0.68, in females 0.65 to 0.75. Rays prominent . . . . *Lampsilis ovata* (p 110, Pl. 9, Figs. 1–6).

Shell elliptical and not relatively high. Height/length 0.50 to 0.62 in both sexes. Females swollen posteriorly. Rays prominent in many specimens, but partly or completely obscure in others . . . . *Lampsilis radiata siliquoidea* (p 105, Pl. 10, Figs. 1–5).

Subfamily Ambleminae Rafinesque

Ambleminae (correction of Amblemidia) Rafinesque, 1820: *Ann. Gén. Sci. Phys.*, Brussels, *5*(13): 310 (Binney & Tryon reprint, 1864: 54). Type genus: *Amblema* Rafinesque, 1820.

Shells large and solid in most species; sculpturing well-developed, moderate, or absent; hinge teeth complete and strong. Sexual dimorphism in shell characters not apparent (except in *Tritogonia*). Tachytictic or short-term breeders, the females retaining the glochidia in the marsupia for only a few days or weeks during the summer. Marsupia formed by all 4 gills or by 2 outer gills only, but in either case the whole gill serving as the marsupium. Water tubes not divided in the gravid female. Glochidia subelliptical or subcircular and without hooks.

Frierson (1927: 25–64) recognizes 235 North American species and numerous subspecies within genera now considered to belong to this subfamily. The number of valid species may be much smaller however. Ambleminae is used in the present work following Morrison (1956: 16) and in preference to Unioninae of Ortmann (1911: 329) and of most subsequent authors. Geologic range: Triassic to Recent (Haas *in* Moore, 1969: N 415).

Genus *Fusconaia* Simpson

Fusconaia Simpson, 1900: *Proc. U.S. Nat. Mus.*, *22*: 784. Type species: *Unio trigonus* Lea, by original designation.

Shells round, rhomboid, triangular, or short elliptical, with a moderate posterior ridge; beaks high and full, curved inward and forward and sculptured with a few coarse, parallel ridges which curve upward posteriorly; disc, posterior ridge and posterior slope unsculptured; hinge plate of moderate width; pseudocardinals heavy and strong; nacre white, salmon, or purple. Sexual dimorphism in shell characters lacking. All 4 gills are marsupial.

Fusconaia contains approximately 15 species and numerous " subspecies ". All except *F. flava* are confined to the Mississippi River and the Gulf of Mexico drainage areas. This genus needs revision, as do most of the other genera in the Unionidae. Geologic range: Pleistocene to Recent.

Fusconaia flava (Rafinesque)

Pig Toe; Plate 1, Figs. 1, 2; Map 2.

Obliquaria flava Rafinesque, 1820: *Ann. Gén. Sci. Phys.* Brussels, *5*(13): 305, pl. 81: 13, 14 (Binney & Tryon reprint, 1864: 49). Type locality: " Les petites rivières se jetant dans le Kentucky, Saltriver et Greenriver."

? *Unio undatus* Barnes, 1823: *Amer. J. Sci.*, *6*: 131, pl. 4: 4. Type locality: " Ouisconsin and Fox Rivers."

? *Unio rubiginosus* Lea, 1830: *Trans. Amer. phil. Soc.*, *3*: 427, pl. 8: 10. Type locality: " Ohio."

? *Unio trigonus* Lea, 1834: *Trans. Amer. phil. Soc.*, *4*: 110, pl. 16: 40. Type locality: " Ohio River at Cincinnati [and] Ohio River at Louisville."

? *Fusconaia flava* var. *parvula* Grier, 1918: *Nautilus*, *32*: 11. Figured by Baker, 1928b: pl. 39: 1–5. Type locality: " Big Bend, Presque Isle Bay, Lake Erie [Pennsylvania]."

? *Fusconaia undata wagneri* Baker, 1928: *Fresh Water Mollusca of Wisconsin. 2* (Pelecypoda): 64, pl. 40: 1–3. Type locality: " Lake Pepin, near Lake City, Minn."

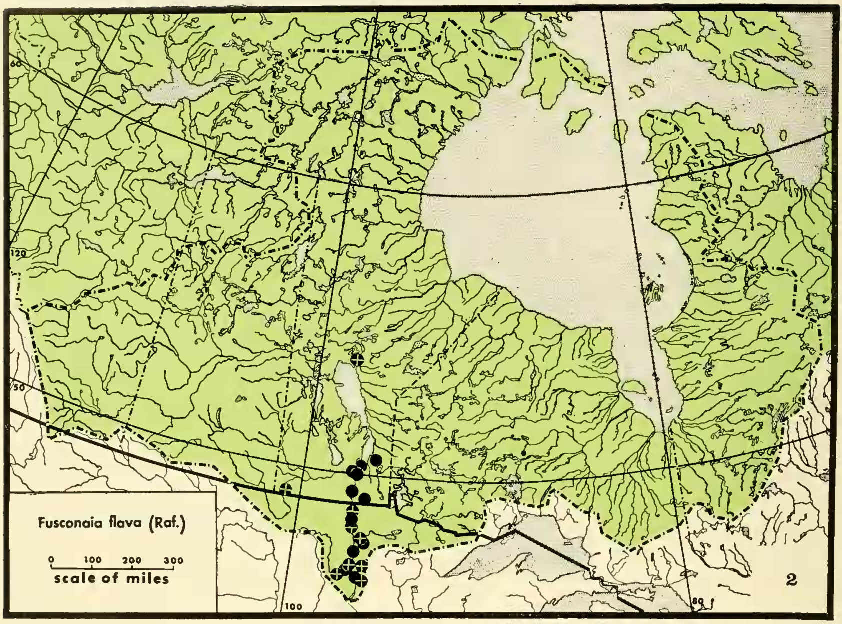
Diagnosis: Shell sub-triangular, without prominent sculpturing, short and heavy, and with relatively large and thick hinge teeth.

Description: Shell medium-sized (up to about 4 inches long), triangular-ovate, bluntly pointed post-basally, rather heavy, strong, thickened anteriorly, and somewhat compressed. Posterior ridge rounded but prominent. Periostracum brown or blackish, sometimes obscurely rayed, roughened by the growth lines but with annual growth rests poorly defined. Beaks inflated, slightly elevated, and sculptured with three to five small, sub-concentric bars (see Pl. 15, Fig. 1). Shell unsculptured except for lines of growth and beak sculpture, the latter often obliterated. Pseudocardinal teeth large, heavy, 1 in the right valve and 2 in the left, and with prominent, irregular grooves and ridges which articulate with corresponding ridges and grooves in the other valve. A small additional pseudocardinal tooth is also present in the right valve anterior to the major tooth. Lateral teeth heavy, moderately long, 1 in the right valve and 2 in the left. Nacre white and in some specimens suffused with pale blue or salmon pink. Muscle scars deeply impressed, especially anteriorly, and pallial line well marked.

Measurements:

The following measurements are used for all Pelecypoda. L=length measured parallel to the long axis of the shell. H=height measured perpendicular to the long axis. W=width of both valves with valves appressed. All measurements are in mm unless otherwise stated.

Feature	N	Range	Mean	$S.E._M$	S.D.
Red River, Abercrombie, N.D.					
L, mm	4	97·2 — 103·3	100·5	—	—
H/L	4	0·729— 0·791	0·766	—	—
W/L	4	0·393— 0·452	0·427	—	—
Red River, St. John Baptiste, Man.					
L, mm	7	52·5 — 66·7	59·4	—	—
H/L	7	0·747— 0·835	0·774	0·013	0·034
W/L	7	0·392— 0·446	0·421	0·007	0·018
Assiniboine River, western city limits of Winnipeg, Man.					
L, mm	9	56·4 — 71·5	64·6	—	—
H/L	9	0·752— 0·831	0·794	0·010	0·029
W/L	9	0·401— 0·458	0·429	0·008	0·023



Records:

Red River system. Red River: Abercrombie, N.D.; 3 mi W of Neilsville, Minn.; 2 mi NE of Drayton, N.D.; and St. John Baptiste, Man. (all this survey). Sand Hill River, Climax, Minn. (this survey). Sheyenne River: 1 mi E of Kindred, N.D. (this survey) and Argusville, N.D. (Ortmann, 1919: 17). Also Red River in United States; Otter Tail, Buffalo, Wild Rice, Sand Hill, and Red Lake rivers in Minnesota; and Sheyenne River in North Dakota (Cvancara, 1967: 189). "Red River" [Otter Tail River] below Fergus Falls, Minn. (as "*Quadrula rubiginosa*") and Otter Tail Lake outlet, Minn. (as "*Quadrula coccinea*") (both Wilson & Danglade, 1914: 12). Red Lake River, Minn. (Dawley, 1947: 679). Souris River, Man. (Mozley, 1938: 122). Roseau River, 8 mi N of Tolstoi, Man. (this survey). Assiniboine River: western edge of Winnipeg, Man.; 8 mi W of Winnipeg; and 12 mi NW of St. Francis Xavier, Man. (all this survey).

Nelson River system. Lake Winnipeg, below Fort Alexander and Elk Island (mouth of Winnipeg River) (1883, R. Bell!). Nelson River (Mozley, 1938: 122).

Distribution: Ohio-Mississippi River system from Oklahoma and Tennessee (Ortmann, 1919: 18) to Minnesota and Pennsylvania. St. Lawrence River system from Wisconsin to New York and southern Ontario. Red River of the North, its tributaries, Lake Winnipeg and Nelson River. In Canada it is relatively uncommon and restricted in distribution, occurring only in the Lake Erie, Lake St. Clair, and Lake Huron drainage areas and in parts of the Red River—Nelson River system.

Biology and Ecology: During this survey *Fusconaia flava* was found only in rivers over 40 ft wide, with a slow or moderate current, with a bottom of mud or sand, with or without gravel and rocks, and with the vegetation sparse or of medium density. At each locality it constituted a minor element (approximately 2% to 5%) of the relatively

rich unionid faunae totalling from four to nine species. In all cases but one, these faunae were composed principally of *Lampsilis radiata siliquoidea* or *Anodonta grandis grandis*. At the single anomalous station (Red River at Abercrombie ,N.D.), *F. flava* constituted 20% of the unionid fauna seen and ranked second in dominance only to *Amblema plicata* (Say).

The anatomy and reproduction of *Fusconaia flava* have been discussed by Ortmann (1911: pl. 89, 1919: 15) and by Baker (1928b: 54). The soft parts are yellowish and orange and the glochidia are hookless, subovate, and measure 0·15 mm in height and width. The breeding season in Pennsylvania occurs from May to August but its duration in the Canadian Interior Basin is unknown. All the specimens were gathered during the first 2 weeks in August of 1961 and 1964, and none were found to be gravid. The host fish are also unknown.

Remarks: Several names, e.g., *rubiginosa* Lea, *undata* Barnes, *trigona* Lea, *wagneri* Baker, and *parvula* Grier (see " Synonymy ") are in use for taxa of various levels all related to *Fusconaia flava*. They differ from typical *F. flava* in obesity, general outline, and tooth morphology. Most of them also differ in ecology, *flava* being considered as typical of small streams, *rubiginosa*, *undata*, and *trigona* of larger streams, and *wagneri* and *parvula* of lakes. The most recent authors to discuss these taxa in detail are Ortmann (1919: 19) and Baker (1928b: 56), who differ widely in their opinions. The status of these names cannot be decided on the basis of the material from the Canadian Interior Basin, but it is perhaps significant that *F. flava* is the only form to occur there or in southern Ontario (excluding the Great Lakes proper) regardless of stream size. The Red River in Manitoba, for example, is certainly a large river and should be expected to support much more inflated specimens than actually occur there.

Two explanations for this anomaly appear reasonable. Perhaps more than 1 species exists within the *Fusconaia flava* group and only *F. flava* (*s. str.*) has managed to traverse the filter bridges involved and to invade the Canadian Interior Basin and southern Ontario. What seems a more likely explanation, however, is that large streams in relatively warmer regions often provide optimum conditions for the growth and development of *F. flava* and there it becomes more obese. Any departure from this environment (small streams in the same climatic belt or small or large streams in colder regions) may produce more compressed, rather depauperate individuals.

Genus *Quadrula* Rafinesque

Quadrula Rafinesque, 1820: *Ann. Gén. Phys.*, Brussels, *5*(13): 305 (as subgenus of *Obliquaria*) (Binney & Tryon reprint, 1864: 49). Type species: *Obliquaria quadrula* Rafinesque, by tautonomy.

Shells triangular, quadrate, or rhomboid; solid and inflated; with prominent umbones which are characteristically sculptured with a few coarse, irregular, subparallel ridges that are enlarged where they cross the posterior ridge; posterior ridge ordinarily well-developed; disc sculptured in most species; periostracum dark and rayless or obscurely rayed; hinge plate heavy, wide, and flattened; pseudocardinal teeth thick and irregular; laterals double in the left and single in the right valve; beak cavities deep and narrow. Sexual dimorphism in shell characters absent. All 4 gills are marsupial throughout, the whole smooth and pad-like, and the species are tachytictic.

Approximately a dozen species occurring in the St. Lawrence River, Mississippi

River and Gulf of Mexico drainage areas are now classified under *Quadrula* (*s. str.*). *Q. quadrula* is the only 1 which has penetrated the Canadian Interior Basin. Geologic range: Pleistocene to Recent.

Quadrula quadrula (Rafinesque)

Maple Leaf; Plate 1, Figs. 3, 4; Map 3.

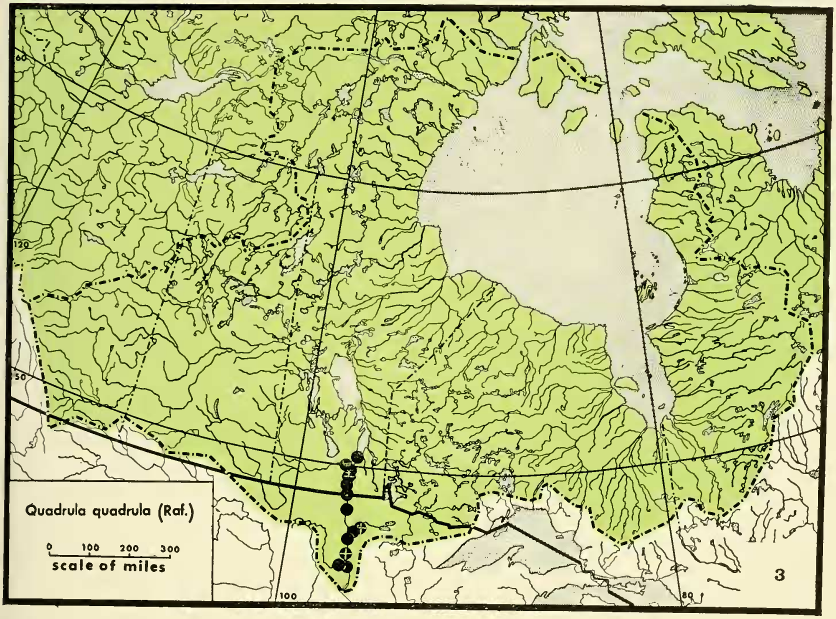
Obliquaria quadrula Rafinesque, 1820: *Ann. Gén. Sci. Phys.*, Brussels, *5*(13): 307 (included under "Sous-Genre, Quadrula") (Binney & Tryon reprint, 1864: 51). Type locality: "dans l'Ohio."
Quadrula quadrula bullocki Baker, 1928 : *Fresh Water Mollusca of Wisconsin. 2* (Pelecypoda) 87, pl 46: 1-3. Type locality: "Fox River near De Pere, Wisconsin."

Diagnosis: Shell subovate, truncated posteriorly, with 2 radiating rows of pustules on each valve, relatively short and heavy, and with moderately large hinge teeth.

Description: Shell medium-sized (up to about 5 inches long), quadrate-ovate, truncate posteriorly, moderately strong, and thickened anteriorly. Periostracum brownish to yellowish or yellowish-green, with narrow rays, and with fine lines of growth and well-marked growth rests. Beaks subinflated and sculptured with tiny pustules (see Pl. 15, Fig. 2). Shell sculptured with irregular, small to rather large nodules principally concentrated in 2 radial bands on each shell, 1 at the posterior ridge and 1 near the centre of the valve. Posterior slope also sculptured with numerous small pustules or short, curved, elongate ridges oriented perpendicular to the lines of growth or both. Pseudocardinal teeth rather large, sub-triangular, sharply acute, and serrated, 2 in the right valve (the anterior one smaller) and 2 in the left. Lateral teeth well developed but rather short, 1 or 2 in the right valve and 2 in the left. Nacre white. Anterior muscle scars deeply impressed, posterior muscle scars and pallial line shallow but well marked.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Red River, 3 mi W of Nielsville, Minn.					
L, mm	16	45·3 —102·9	61·5	—	—
H/L	16	0·716— 0·809	0·773	0·006	0·023
W/L	16	0·422— 0·483	0·445	0·005	0·020
Red River, 2 mi NE of Drayton, N.D.					
L, mm	17	58·8 —117·5	84·0	—	—
H/L	17	0·660— 0·829	0·750	0·010	0·040
W/L	17	0·401— 0·469	0·430	0·004	0·017
Red River, St. John Baptiste, Man.					
L, mm	25	44·1 — 83·4	67·1	—	—
H/L	25	0·724— 0·834	0·788	0·005	0·026
W/L	25	0·404— 0·500	0·453	0·004	0·022



Records:

Red River system. Red River: Abercrombie, N.D.; 3 mi W of Nielsville, Minn.; 2 mi NE of Drayton, N.D.; (all this survey); Emerson, Man. (Nat. Mus. Can.); St. John Baptiste, Man.; Aubigny, Man. (both this survey) and Winnipeg, Man. (Mozley, 1938: 122). Sand Hill River, Climax, Minn. (this survey). Red Lake River, Minn. (Cvancara, 1967: 189). Sheyenne River: 1 mi E of Kindred, N.D. (this survey) and Argusville, N.D. (Ortmann, 1919: 42). Roseau River, 8 mi N of Tolstoi, Man. (this survey). Assiniboine River: western edge of Winnipeg, Man. and 8 mi W of Winnipeg (both this survey).

Nelson River system. Fort Garry, Man. [Lake Winnipeg], (1883, R. Bell!).

Distribution: Much like *Fusconaia flava*, viz.: Ohio-Mississippi River system from Texas and Alabama to Minnesota and Pennsylvania, St. Lawrence River system from Wisconsin to western New York and southern Ontario, and Red River of the North and some of its tributaries. The distribution of *Quadrula quadrula* in Canada is restricted to the Lake Erie and Lake St. Clair drainage areas and the Red River system.

Biology and Ecology: The ecology of *Quadrula quadrula* in the Canadian Interior Basin is very similar to that of *Fusconaia flava*. *Q. quadrula* occurred only in rivers of approximately 40 ft width or greater and in which the current was slow to moderate, the bottom was mud or sand with or without clay, rocks, or gravel, and the vegetation was sparse to moderately dense. It was found to be ordinarily uncommon, but comprised up to 28% of the unionids seen at 1 locality (Red River near Drayton, N.D.). At all stations but 2 the unionid fauna was dominated by *Lampsilis radiata*

siliquoidea. At the 2 exceptional localities (Red River near Nielsville, Minn. and Sand Hill River, Climax, Minn.) the most abundant species was *Anodonta grandis grandis*.

Discussions of the anatomy and reproduction of *Quadrula quadrula* have been given by Baker (1928b: 85) and by Ortmann (1912: 253, 1919: 41). According to Baker the soft parts are whitish. Specimens collected on August 3, 1964 in the Red River at Abercrombie, N.D. and in the Sheyenne River near Kindred, N.D. had orange to orange-red soft parts. The glochidia are reported to be semi-elliptical, 0 085 mm in height, and 0·078 mm in length. The breeding season in Iowa and Kansas extends at least from June to August but its duration in the Canadian Interior Basin is unknown. All specimens collected during this survey were gathered in the first 1½ weeks in August and none were found to be gravid. The fish host for *Q. quadrula* has not yet been determined.

Remarks: Neel (1941) has studied the variation of this species and has concluded that only 1 subspecies in addition to *Quadrula quadrula* (*s. str.*) is worthy of recognition. This is *Q. q. apiculata* (Say) [=*Q. q. speciosa* (Lea)] from the Gulf of Mexico drainage area. *Q. q. bullocki* Baker was not cited specifically but its synonymy with *Q. q. quadrula* is implied. I agree with this.

Quadrula quadrula bullocki is characterized by Baker as " being more elongated and compressed [W/L= 0·40–0·51 in examples cited], and usually less pustulous, and with more depressed umbones. It appears to be the form of small rivers and streams, whereas *Q. q. quadrula* [W/L=0·51–0·62 in examples cited] is confined to the larger rivers . . . a true ecological or physiographic variety." Here we see a fundamental difference between Baker's concept of the subspecies and the modern concept as defined by the International Code of Zoological Nomenclature [1961, Article 45 (d)]. Baker used trinomial combinations to indicate true subspecies and also to indicate infrasubspecies. In many cases it is not clear from his text which he had in mind. Most of his trinomials have been uncritically perpetuated in the literature as subspecies, however, and each one must be re-examined to determine its proper taxonomic position.

All Canadian specimens of *Quadrula quadrula* seen are similar to *bullocki* in relative inflation (W/L), the chief character used by Baker. (The other distinguishing characters of *Q. q. bullocki* are variations common throughout the range of the species and no one has suggested that they are diagnostic). The populations of the Red River drainage area, the Lake Erie and Lake St. Clair drainage areas and the Fox River drainage area in Wisconsin were derived independently from separate parts of the Mississippi—Ohio River system. Unless we accept the unlikely possibility that parallel evolution occurred in all 3 areas and led to the development of the same morphological subspecies in each case, we must presume that we are dealing with ecophenotypes. This is a situation similar to that seen in *Fusconaia flava* and *Amblema plicata* and is another example of what appears to be a general trend among unionids (and especially within the Ambleminae): that northern populations of widespread species are often more compressed than their southern large-stream counterparts, regardless of the size of the stream occupied in the north.

Genus *Amblema* Rafinesque

Amblema Rafinesque, 1820: *Ann. Gén. Sci. Phys.*, Brussels, *5*(13): 314 (Binney & Tryon reprint,

1864: 57). (*Nomen conservandum*). Type species: *Amblema costata* Rafinesque [= *Unio plicata* Say, 1817 (*nomen conservandum*)], subsequent designation, Walker, 1918: 47. Not *Amblema* Rafinesque, 1819 (*nomen dubium* and *suppressum*). See ICZN Opinion 840.

Not *Crenodonta* Schlüter, 1838: *Kurzgefasstes Verzeichniss meiner Conchyliensammlung* (etc.). Halle. p 33. Type species: *Crenodonta securis* (Deshayes) [now *Plagiola securis* (Desh.)], subsequent designation, Herrmannsen, 1852: 38. The more recent subsequent type designation of *Unio plicatus* Say (by Simpson, 1900: 766) is invalid (ICZN Opinion 840).

Shells quadrate to ovate, slightly alate, slightly thickened to thick, and sculptured with heavy, subparallel, diagonal folds extending over most of the shell. Beaks prominent and with coarse concentric or double-looped ridges. Periostracum brown to blackish and without rays. Hinge teeth strong to massive. Sexual dimorphism in shell characters lacking. Marsupia occupying all 4 gills. Tachytictic.

Approximately 8 species and subspecies are members of this genus and all except *Amblema plicata* are restricted to the Mississippi River or the Gulf of Mexico drainage areas, or both. Geologic range: Lower Cretaceous to Recent.

Amblema plicata (Say)
Three Ridge; Plate 1, Figs. 5, 6; Plate 2, Figs. 1, 2; Map 4.

Unio plicata Say, 1816: *Nicholson's Encyclopedia*, 1st Amer. ed., art. Conchology, pl. 3: 1 (Binney reprint, 1858: 50). Type locality: " Lake Erie."

Amblema costata Rafinesque, 1820: *Ann. Gén. Sci. Phys.*, Brussels, *5*(13): 315, pl. 82: 13, 14 (Binney & Tryon reprint, 1864: 58). Type locality: " l'Ohio " [rare], " les petites rivières du Kentucky " [common].

Unio hippopaeus Lea, 1845: *Proc. Amer. phil. Soc.*, *4*: 163 (Latin description only); 1848: *Trans. Amer. phil. Soc.*, *10* (art. 4): 67, pl. 1: 1, Type locality: " Lake Erie."

Diagnosis: Shell ovate, thick, massive, medium to large in size and sculptured with 3 or 4, usually prominent, diagonal ridges.

Description: Shell medium to large (up to about 6 inches long), subtruncate posteriorly in most specimens, medium-heavy to heavy, strong, thickened anteriorly, and slightly compressed. Posterior ridge not well defined. Periostracum brown or blackish and roughened by concentric lines and by growth annuli. Beaks slightly elevated, located near the anterior end, and sculptured with about 5 low, subconcentric, ridges (Pl. 15, Fig. 3). Shells of most specimens bearing 3 or 4 prominent, rounded corrugations directed posterio-ventrally and extending over most of the surface. These ridges are reduced or lacking in some specimens. Pseudocardinal teeth thick and heavy, subtriangular, erect, rounded, and serrated, 2 in the right valve (the anterior 1 small) and 2 in the left. Lateral teeth usually well developed, quite straight and of medium length, 1 in the right valve and 2 in the left. Nacre white, iridescent posteriorly. Anterior muscle scars deeply impressed and roughened, posterior muscle scars and pallial line shallow but well marked.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Red River, Abercrombie, N.D.					
L, mm	13	122·9 —155·5	141·9	—	—
H/L	13	0·654— 0·764	0·695	0·008	0·029
W/L	13	0·358— 0·430	0·403	0·006	0·022

Feature	N	Range	Mean	S.E.$_M$	S.D.
Red River, St. John Baptiste, Man.					
L, mm	40	67·2 — 98·7	82·7	—	—
H/L	40	0·686— 0·797	0·729	0·004	0·024
W/L	40	0·341— 0·448	0·389	0·004	0·028
Assiniboine River, Winnipeg, Man. at western city limits.					
L, mm	42	77·3 —120·1	92·3	—	—
H/L	42	0·653— 0·786	0·726	0·005	0·035
W/L	42	0·345— 0·463	0·407	0·004	0·025

Records:

Winnipeg River system. Whitemouth River near Whitemouth, Man. (this survey).

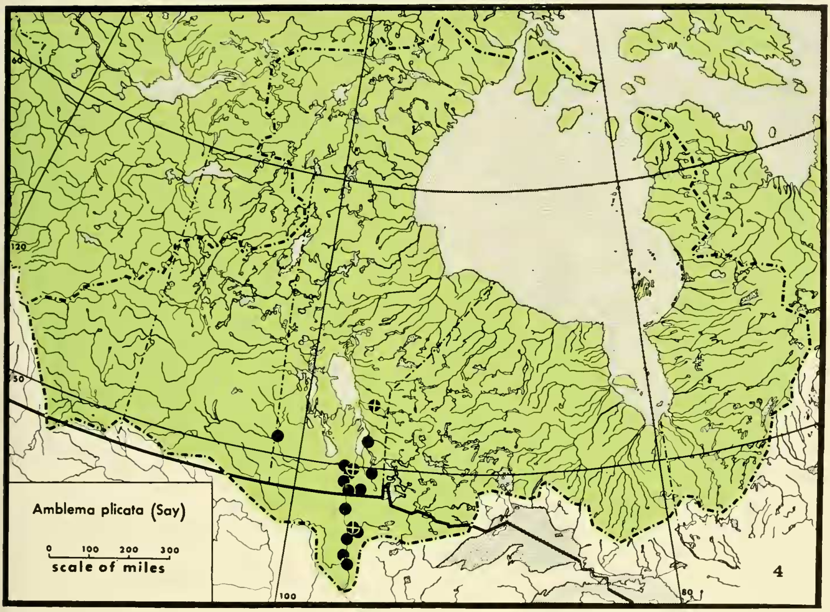
Red River system. Red River: Abercrombie, N.D.; 3 mi W of Nielsville, Minn.; 2 mi NE of Drayton, N.D. (all this survey); Emerson, Man. (Nat. Mus. Can.); St. John Baptiste, Man.; Aubigny, Man.; 1 mi S of St. Norbert, Man. (all this survey), and Winnipeg, Man. (Mozley, 1938: 122). Red Lake River, Minn. (Dawley, 1947: 679, and Cvancara, 1967: 189). Sand Hill River, Climax, Minn.; Sheyenne River, 1 mi E of Kindred, N.D. (both this survey). Otter Tail River, Minn.; Sheyenne River, N.D.; and Wild Rice River, Minn. (Cvancara, 1967: 189). Roseau River, 8 mi N of Tolstoi, Man.; La Salle River, St. Norbert, Man. Assiniboine River: western edge of Winnipeg, Man.; 8 mi W of Winnipeg; 12 mi NW of St. Francis Xavier, Man. (all this survey); and Millwood, Man. (1889, J. B. Tyrrell!).

Nelson River system. Black River near Lake Winnipeg (1883, R. Bell!). Berens River, Englishman's Rapid, Man., depth of 12 metres (Mozley, 1938: 122).

Distribution: Ohio-Mississippi River system from Tennessee and Oklahoma to Pennsylvania and Minnesota. Upper St. Lawrence River system (except Lake Superior and tributaries) from Wisconsin to New York and Southern Ontario. (South of Lake Ontario it occurs only in the Erie Barge Canal of New York and some contiguous waterways). Red River of the North, its tributaries, and some other tributaries of Lake Winnipeg.

Biology and Ecology: In the region under discussion *Amblema plicata* has been found only in rivers over 40 feet in width. Current was slow or moderate and substrates were various, i.e., clay, mud, sand, or gravel. Vegetation was sparse to moderate in all these habitats. At the localities in which it occurred it constituted from 2 to 27% of the unionid fauna. It was the most abundant species at only 1 locality: the Red River at Abercrombie, N.D.

The anatomy and reproduction of *Amblema plicata* have been discussed by Ortmann (1911, 1919) and by Baker (1928b). The glochidia are suboval, without hooks, and measure approximately 0·21 mm in length and 0·22 mm in height (Ortmann, 1911: 247). In Pennsylvania it breeds from May to July. In the Canadian Interior



Basin the breeding season is probably slightly later, although none of the specimens collected during this survey (all gathered in early August) were gravid. Of the host fish listed by Coker *et al.* (1921: 152) and Baker (1928b: 74) only 3 occur in the Red River system, viz.: sauger, *Stizostedion canadense* (Smith); pike, *Esox lucius* L.; and red-ear or pumpkinseed sunfish, *Lepomis gibbosus* L. Additional common, closely-related species such as the yellow pikeperch, *Stizostedion vitreum* (Mitchill) and the yellow perch, *Perca fluviatilis flavescens* (Mitchill) may also prove to be hosts for *A. plicata*.

Remarks: It is generally agreed among malacologists that unionids occurring in many parts of Lake Erie are stunted by their environment and that they are not genetically distinct from larger forms occurring in nearby streams (see, e.g., Brown *et al.*, 1938). This is a general phenomenon exhibited by several species. In Canada, for example, some northern tributaries of the Great Lakes containing species which originated in the Ohio-Mississippi River drainage areas have apparently derived their faunae from stunted Great Lakes populations. The robust individuals which occur there are typical of southern tributaries of the Great Lakes and northern parts of the Ohio-Mississippi River drainage.

It is quite clear that *Unio plicata* Say, 1817, and *Amblema costata* Rafinesque, 1820, represent the same species. The Rules require that priority in such a case should prevail and therefore the name *plicata* must be used. The name *costata* thus becomes obsolete or, at best, merely an infra-subspecific

term for the ecophenotype occurring in Lake Erie. This conclusion has been published previously by Clarke & Clench (1966: 341), but without discussion. The same decision has also been reached independently by Stein (1963) and is implied by the usage of Stansbery (1964). *Amblema plicata* (Say) is now on the Official List of Specific Names in Zoology (ICZN, Opinion 840).

Unio hippopaeus Lea is clearly a synonym of *Amblema plicata* (Say). In addition, it is probable that *U. peruviana* Lamarck and *U. rariplicata* Lamarck are also ecophenotypes of *plicata*, but this cannot be decided on the basis of Canadian Interior Basin material. However, we can at least conclude that only 1 species (without additional subspecies) of *Amblema* occurs in the Hudson Bay and in the St. Lawrence River drainage areas. It appears probable that this conclusion applies to most, and perhaps all, the Ohio-Mississippi River drainage areas as well.

Amblema plicata from the Canadian Interior Basin shows the same extreme compression observed in *Fusconaia flava* and *Quadrula quadrula*.

Genus *Elliptio* Rafinesque

Elliptio Rafinesque, 1819: *J. Phys. Chim. Hist. nat.*, etc., *88*: 426 (*nomen dubium*). Rafinesque, 1820: *Ann. Gén. Sci. Phys.*, Brussels, *5*(13): 291 (Binney & Tryon reprint, 1864: 29, 37). Type species: *Unio nigra* Rafinesque [= *Unio crassidens* Lamarck], by subsequent designation, Ortmann, 1912: 266. (The type designation by Simpson (1900: 700) of *Unio crassidens* Lamarck is invalid because *crassidens* was not included in *Elliptio* by Rafinesque in 1820). According to H. B. Baker (1964: 33) *Elliptio* is feminine.

Shells slightly thickened to heavy and ponderous; lanceolate, ovate, subrhomboid, or subtrapezoid; commonly slightly biangulate posteriorly; and surface smooth or corrugated. Beak sculpture consisting of a few ridges that are nearly parallel to the growth lines or slightly double-looped. Periostracum rayless or rayed; hinge plate narrow; and hinge teeth well developed. Sexual dimorphism of shell characters lacking. Marsupia forming thick, smooth pads that occupy the whole length of the outer gills only. Tachytictic.

Frierson (1927: 25) lists 87 species and subspecies in *Elliptio* (*s. str.*), but this list should be drastically reduced. I believe that nearly 3/4 of these taxa, particularly many from the southern Atlantic and the Gulf of Mexico drainage areas, are invalid. The genus is distributed over nearly all eastern North America. Geologic range: Cretaceous (?) to Recent.

Elliptio complanata (Solander)

Eastern Elliptio; Plate 3, Figs. 1–6; Map 5.

Mya complanata Solander, 1786: *Portland Cat.*, *11*, lot 2190. Type locality: Maryland.

Diagnosis: Shell medium-sized, typically subtrapezoidal, compressed and commonly with purple nacre but extremely variable.

Description: Shell up to about 4 inches long, subelliptical to subtrapezoidal, and of medium strength and thickness. In most specimens the posterior margin is obliquely subtruncate and the posterior ridge is low and rounded. Periostracum greenish-brown to brownish-black, obscurely rayed in some specimens (especially in juveniles), and roughened by concentric threads and fine ridges. Beak sculpture composed of concentric ridges (see Pl. 15, Fig. 4). Pseudocardinal hinge teeth prominent, erect, and serrate, single in the right valve and double in the left. Lateral teeth well developed, long, and slightly

curved, also single in the right valve and double in the left. Nacre purple in the majority of specimens but may be orange, white, or some intermediate shade. Anterior muscle scars impressed; posterior muscle scars and pallial line not impressed but clearly delineated.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Lac Dubuisson, 5 mi NW of Val d'Or, Que.					
L, mm	30	68·6 —87·8	77·5	—	—
H/L	30	0·503— 0·585	0·541	0·004	0·020
W/L	30	0·238— 0·295	0·269	0·003	0·016
O'Sullivan River, ½ mi N of Miquelon, Que.					
L, mm	25	61·0 —99·0	75·0	—	—
H/L	25	0·463— 0·540	0·504	0·004	0·023
W/L	25	0·233— 0·312	0·268	0·004	0·022

Records:

Nottaway River system. O'Sullivan River, ½ mi N of Miquelon, Que. Bell River, 33 mi N of Senneterre, Que. Taschereau River near mouth 40 mi N of Senneterre, Que. (all this survey).

Harricanaw River system. Lac Dubuisson, 5 mi NW of Val d'Or, and Lac la Motte, 25 mi NW of Val d'Or, Que. (both this survey).

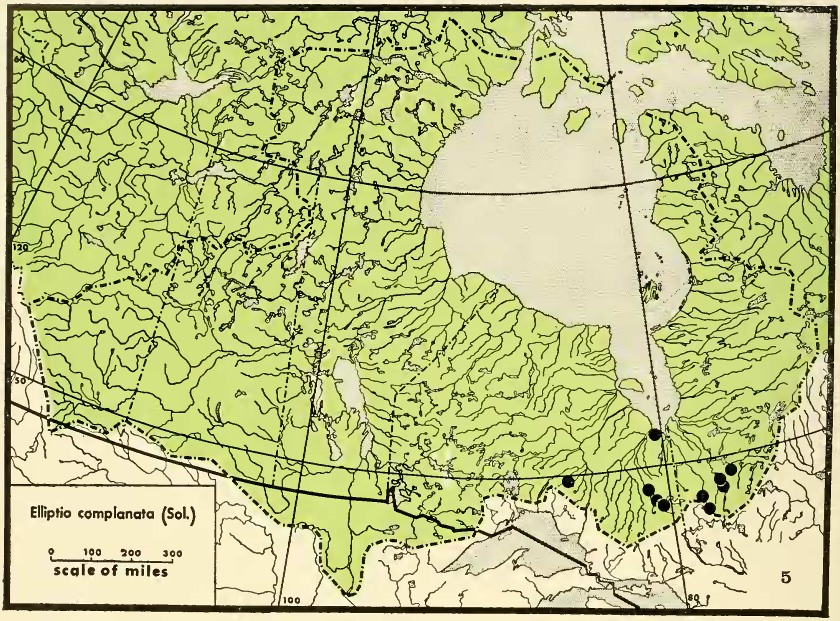
Moose River system. Frederick House River, 6 mi N of Cochrane, Ont. Black River at Matheson, Ont. Wilson Lake, 1½ mi S of Nellie Lake, Ont. Moose River at Moose Factory, Ont. (all this survey).

Albany River system. Klotz Lake, 30 mi E of Longlac, Ont. (this survey).

Distribution: *Elliptio complanata* is distributed throughout the Atlantic drainage from the Gulf of St. Lawrence to Georgia; in the Great Lakes of the St. Lawrence River system and their tributaries (except Lake Michigan and most of Lake Erie); and in the Canadian Interior Basin in the Nottaway, Harricanaw, Moose and Albany River systems. The record "Saskatchewan River" given by Dall (1905: 133) is almost certainly incorrect.

Biology and Ecology: In the Canadian Interior Basin as elsewhere in its range, *Elliptio complanata* occurs in many kinds of habitats. It occurs in large and small lakes, in large and medium-sized rivers, on bottoms varying from mud or clay to coarse gravel, and associated with vegetation which may be moderately heavy to quite sparse. In relative abundance it varied from 1 to over 75% of the unionid fauna at any single locality. Its usual associates are *Anodonta grandis* and *Lampsilis radiata siliquoidea*.

The anatomy of *Elliptio complanata* has been discussed by Ortmann (1911:



269) and Reardon (1929: 10). The breeding season in Pennsylvania is from April to July or August. The glochidia are subovate, without hooks, and measure about 0·20 mm long and 0·19 mm high. All specimens of *E. complanata* obtained during this survey were collected between July 26 and August 27 (over several years) and none were found to be gravid. According to Lefevre and Curtis (1912: 168) and Matteson (1948: 707) the yellow perch, *Perca fluviatilis flavescens* (Mitchill), serves as a host for *E. complanata*.

Remarks: Although *Elliptio complanata* is abundant and ubiquitous throughout the Atlantic drainage, in the Canadian Interior Basin it is uncommon. The only localities in that region where it has been collected in abundance are Lac Dubuisson [=Lac Montigny] near Val d'Or, Que., and O'Sullivan River near Miquelon, Que. The known range of its host fish, *Perca fluviatilis flavescens*, corresponds well with the range of *E. complanata* in the Canadian Interior Basin, except that the fish extends much farther westward, even reaching into Alberta.

For many years the presence of *Elliptio complanata* in Georgian Bay, in Northern Michigan, and in Lake Superior has been considered anomalous. This was presumed to have been brought about initially by migration into Georgian Bay by way of its post-glacial outlets, the Trent River and the Ottawa River (Walker, 1913; Clarke & Berg, 1959). Although this explanation is reasonable, more northern routes were also available. Migration may have been much later, perhaps from 4000 to 6000 years ago during the hypsithermal period (Deevey & Flint,

1957; Terasmae, 1961), through interdigitating and occasionally interconnecting parts of the St. Lawrence River and southern James Bay drainage areas. Even now the large Albany River system which discharges into James Bay is confluent with Lake Superior through Long Lake and Lake Nipigon. Post-hypsithermal cooling about 3000 years ago could well have reduced the populations of *E. complanata* to, or beyond, their present low levels in the Canadian Interior Basin.

Subfamily Anodontinae Rafinesque

Anodontinae (correction of Anodontidia) Rafinesque, 1820: *Ann. Gén. Sci. Phys.*, Brussels, *5*(13): 316 (Binney & Tryon reprint, 1864: 58). Type genus: *Anodonta* Lamarck, 1799.

Shells small to large, thin to slightly thickened (but not heavy), sculpturing various, and hinge teeth partly reduced to absent. Sexual dimorphism of shell characters not apparent. Bradytictic or long-term breeders, the females retaining the glochidia within the marsupia at least from the fall to the following spring. Marsupia formed by the outer gills throughout their whole length. Water tubes in the gravid female each divided longitudinally into 3 tubes, only the middle 1 being used as an ovisac. Glochidia semicircular or subtriangular and with hooks.

Approximately 55 North American species are currently recognized as valid. A number of others occur in Eurasia. Two Tribes are recognized in North America, Alasmidontini and Anodontini (Clarke & Berg, 1959). Geologic range· Upper Cretaceous to Recent.

Tribe Alasmidontini

Shells of medium thickness and with or without sculpturing on the posterior slope. Pseudocardinal teeth present and, in many species, prominent. Lateral teeth present or absent.

Genus *Lasmigona* Rafinesque

Lasmigona Rafinesque, 1831: *Continuation of a Monograph of the Bivalve Shells of the River Ohio* (etc.), Philad. p4 (Binney & Tryon reprint, 1864: 78). Type species: *Alasmidonta costata* Rafinesque, by subsequent designation, Simpson, 1900: 664.

Shells medium to large; rather thin to slightly thickened; elliptical, ovate, or subtrapezoid; with or without a dorsal wing; with costae on the posterior slope or on the wing or entirely smooth; periostracum commonly with rays. Hinge teeth characteristic: pseudocardinal teeth prominent, interdental projection well developed in most species, and lateral teeth commonly shortened or much reduced. Beak sculpture consisting of strong double-looped bars. Sexual dimorphism in shell characters occurs in some species but it is not well marked and is unreliable for external sex recognition. In other species males are absent or very rare. The marsupia are thick, pad-like, and fill the outer gills and the species are bradytictic, i.e., long-term breeders.

About 6 species of *Lasmigona* are known. These occur in the Atlantic, Gulf of Mexico, Ohio-Mississippi River, St. Lawrence River and Hudson Bay drainage areas. Geologic range: Pleistocene to Recent.

Lasmigona costata (Rafinesque)

Fluted Shell; Plate 4, Figs. 3, 4; Map 6.

Alasmidonta costata Rafinesque, 1820: *Ann. Gén. Sci. Phys.*, Brussels, *5*(13): 318, pl. 82: 15, 16 (Binney & Tryon reprint, 1864: 60). Type locality: "la rivière Kentuky."

Lasmigona costata var. *eriganesis* Grier, 1918: *Nautilus*, *32*(1): 10. Type locality: Lake Erie.

Lasmigona costata pepinensis Baker, 1928: *The fresh water Mollusca of Wisconsin*. Pt. 2, p 144, pl. 59: 1, 2. Type locality: "Lake Pepin, Wisconsin."

Lasmigona costata nuda Baker, 1928: op. cit., p 145, pl. 59: 3–6. Type locality: "Red Cedar River, west of Chetek, Barron Co.", Wisconsin.

Diagnosis: Shell medium to large, subrhomboid, moderately elongate, and in most specimens corrugated posteriorly.

Description: Shell medium to large (up to about 5 inches long), subrhomboid to subtrapezoid, moderately thick and strong, typically corrugated posteriorly, and rather compressed. Periostracum rough and brownish to blackish in specimens seen (which are all adult), but presumably, as in the Tennessee River system, paler and with rays in young specimens. Posterior ridge low and indistinct. Posterior slope corrugated with four to eight broad, low ribs (in Hudson Bay drainage specimens examined) intersecting the posterior margin and approximately perpendicular to it. Beak sculpture distinct (Pl. 15, Fig. 5) and rather variable. Pseudocardinal teeth well developed, 1 or 2 in the right valve and 2 in the left. Interdental projection in left valve prominent and rather heavy, articulating with an interdental groove in the right valve. Lateral teeth rudimentary or absent. Nacre bluish-white to white, iridescent, and in some specimens with orange or salmon suffusions.

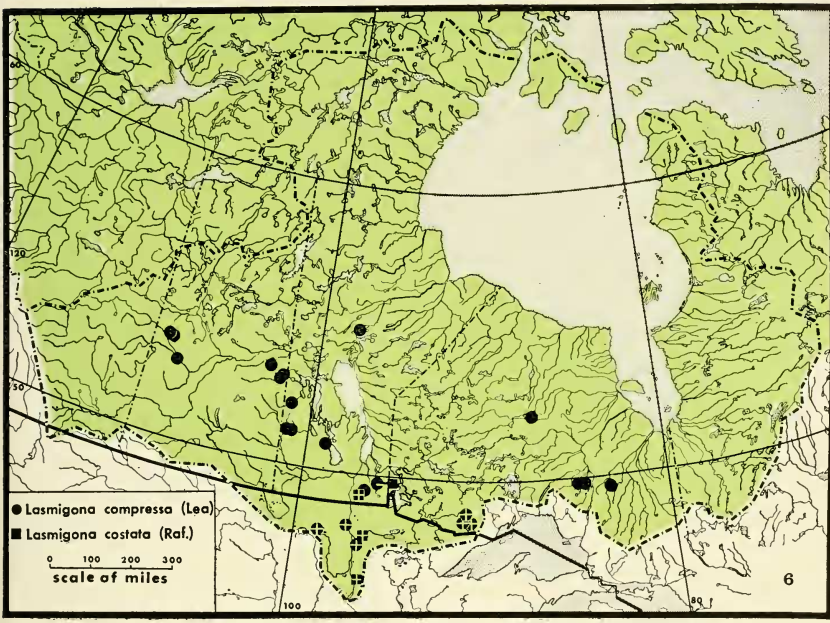
Measurements:

N	Length, mm	Height, mm	Width, mm	H/L	W/L
Birch River at Hwy. 1 near McMunn, Man.					
1	125·3	68·5	38·0	0·547	0·303
2	118·1	63·3	34·7	0·536	0·294
3	116·6	64·4	36·8	0·552	0·316
4	113·6	65·4	38·2	0·576	0·336
5	100·9	54·7	28·0	0·542	0·278
Mean	114·9	63·3	35·1	0·551	0·305

Records:

The only specimens of *Lasmigona costata* found during this survey were those from Birch River in the Winnipeg River system cited above. The lot consisted of 2 living specimens and 3 pairs of empty valves. Six other records from the Canadian Interior Basin, all from the Red River system, are in the literature: Roseau River, Man. (Dall, 1905: 131); Red Lake River, Minn. (Dawley, 1947: 679 and Cvancara, 1967: 189); Little Pine Lake outlet, Minn.; Otter Tail Lake outlet, Minn.; and "Red River" [Otter Tail River], Perham, Minn. (all Wilson & Danglade, 1914: 12).

Distribution: Tombigbee River system, Mississippi ("Simpson", Ortmann, 1919: 130); Mississippi and Ohio River drainages; St. Lawrence River system (primarily in streams) from north of Lake Superior to Lake Champlain and the Ottawa River; and Hudson Bay



drainage area in the Red and Winnipeg River systems (rare). Wilson & Danglade (1914: 12) reported it from 3 of the 5 localities within the Red River system which they visited in 1912. This may indicate that *Lasmigona costata* was much more abundant in that region in 1912 than it is at present.

Biology and Ecology: The single locality in which *Lasmigona costata* was found is a small, slow-flowing river, 25 to 40 feet in width and up to $2\frac{1}{2}$ feet in depth. The bottom was a mixture of rocks, gravel, sand, and mud and vegetation was quite abundant. At this locality *L. costata* comprised 12% of the unionid fauna. Associated species were *Lampsilis radiata siliquoidea* (35%), *Anodonta grandis* (32%), *Lasmigona complanata* (16%) and *Strophitus undulatus* (5%).

The anatomy and reproduction of *Lasmigona costata* have been discussed by Ortmann (1911: 283) and by Baker (1928b: 143). The soft parts are yellowish or orange, with black mantle edges and brown gills. In Pennsylvania the breeding season begins in August and glochidia are held through the winter and are released in May. One of the 2 specimens collected alive at Birch River, on August 20, 1961, was gravid and contained mature glochidia. These were triangular and measured 0·36 mm in length and from 0·38 to 0·40 in height. The natural host fish of *L. costata* is unknown, but Lefevre & Curtis (1912: 158) cite a case of successful metamorphosis on the carp, *Cyprinus carpio* Linnaeus, a fish introduced from Europe by man, probably in 1831 (Mc Crimmon, 1968: 17).

Remarks: Although this species is not known to evolve morphologically distinct local populations in the same bewildering manner as *Anodonta grandis*, distinct local populations do occur. This has been pointed out by Baker (1928b: 145) who applied formal subspecific names to some of them. Many of these variations are probably attributable to water hardness or availability of food and only rarely, as in uncorrugated specimens (i.e., in *Lasmigona costata nuda*), are environmental relationships obscure (see Clarke & Berg, 1959: 34). Smooth forms occur in many, widely separated localities within the range of typical *L. costata*, however, and they cannot constitute a valid subspecies.

Lasmigona compressa (Lea)

Compressed Lasmigona;
Plate 4, Figs. 1, 2; Map 6.

Symphynota compressa Lea, 1829: *Trans. Amer. phil. Soc.*, *3*: 450, pl. 12: 22. Type locality: Ohio and Norman's Kill, Albany, New York.

Unio compressus var. *plebius* C. B. Adams, 1842: [*in*] *Thompson's History of Vermont*, p 166. Type locality: " Middlebury " [Vermont].

" *Lasmigona* (*Platynaias*) *viridis* (Rafinesque) " Ortman, 1919: *Mem. Carnegie Mus.*, *8*(1): 116. See " Remarks " below.

Diagnosis: Shell medium-sized, subrhomboid, compressed, rather thin, smooth, with well-developed hinge teeth and with greenish rays in most specimens.

Description: Shell medium-sized (up to about 4 inches long), subtrapezoid or subrhomboid, quite thin, moderately strong, compressed. Young specimens have a well-developed dorsal projection or " wing." Periostracum yellowish-brown, greenish-brown, or blackish and extensively rayed in most specimens. Posterior ridge low and rounded. Posterior slope compressed. Shell unsculptured except for lines of growth and beak sculpture. Beaks only slightly elevated and prominently sculptured with double-looped, irregular bars (Pl. 15, Fig. 6). Pseudocardinal teeth well developed, narrow, and directed forward, 1 in the right valve and 2 in the left. Interdental projection in left valve prominent and articulating with interdental depression in right valve. Lateral teeth long, straight, and thin, 1 in the right valve and 2 in the left, but in some specimens not well developed. Nacre silvery-white or bluish, iridescent posteriorly, and often cream- or salmon-coloured near the beak cavities.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Turtlelake River, Edam, Sask.					
L, mm	9	47·0 —85·2	63·3	—	—
H/L	9	0·546— 0·617	0·569	0·009	0·026
W/L	9	0·223— 0·261	0·239	0·004	0·013

Feature	N	Range	Mean	S.E.$_M$	S.D.
Fir River, 3 mi S of Hudson Bay, Sask.					
L, mm	5	55·8 —87·1	65·4	—	—
H/L	5	0·534— 0·588	0·564	—	—
W/L	5	0·254— 0·296	0·268	—	—
Nagagami River, 40 mi W of Hearst, Ont.					
L, mm	5	57·2 —70·2	64·7	—	—
H/L	5	0·503— 0·538	0·527	—	—
W/L	5	0·294— 0·306	0·301	—	—
Shekak River, 34 mi W of Hearst, Ont.					
L, mm	2	60·2, 60·4	60·3	—	—
H/L	2	0·591, 0·606	0·598	—	—
W/L	2	0·262, 0·320	0·291	—	—

Records:

Moose River system. Missinaibi River, 20 mi E of Hearst, Ont. (1915, F. R. Latchford!).

Albany River system. Shekak River 34 mi W of Hearst, Ont.; Nagagami River, 40 mi W of Hearst, Ont. (both this survey).

Attawapiskat River system. Pebble River [" Boulder River "], about 170 mi N of Geraldton, Ont. (52°30′N, 87°30′W) (1886, R. Bell!)

Winnipeg River system. Rainy River District, Ont. " Kashapiwigamak Lake " [Deatys Lake]. " Kashapiwigamak River " [Wawiag River]; and between Crooked Pine Lake and Chief Peter Lake (Baker, 1939b: 89). Whitemouth River, Whitemouth, Man. (this survey).

Red River system. Sand Hill River, Minn. and Forest River, N.D. (Cvancara, 1967: 189). Sheyenne River south of Devil's Lake, N.D. (Winslow, 1921: 15). Rat River, 1 1/2 mi S of La Rochelle, Man. Shell River, 6 mi E and 8 mi E of Roblin, Man. (all this survey).

Lake Manitoba - Lake Winnipegosis drainage areas. Woody River, 8 mi N of Swan River, Man. Ebb and Flow Lake, 4 mi NNW of Kinosota, Man. Fir River, 3 mi S of Hudson Bay, Sask. Red Deer River, 4 mi S of Hudson Bay, Sask. (all this survey).

Saskatchewan River system. Carrot River, NW of Arborfield, Sask. (53°15′N, 103°30′W) (1935, R. T. D. Wickenden!). Battle River tributary, 1 mi S of Battleford, Sask. (1964, E. L. Bousfield!). Englishman River, 3 mi NW of Spruce Lake, Sask. Turtlelake River, Turtleford, Sask. (both this survey).

Distribution: Ohio-Mississippi River system from Minnesota to New York and from Nebraska to West Virginia; St. Lawrence River system from Wisconsin to Vermont and Quebec; Hudson River system in New York; and Canadian Interior Basin in

Saskatchewan, Manitoba, North Dakota, Minnesota and Ontario.

Biology and Ecology: During this survey *Lasmigona compressa* was found in rivers of all sizes, but was dominant in only 2 small rivers in Saskatchewan, both less than 50 feet wide. In 1 of these, the Fir River near Hudson Bay, Sask., the bottom was of rocks, gravel, and sand and the current was rapid. In the other, a tributary of the Battle River near Battleford, Sask., the bottom was mud and the current was slow. Other localities supporting sparse populations of this species were rivers ranging from 30 to 200 feet in width, with bottoms of mud, sand, gravel, or rocks, or both and with slow, moderate, or rapid current. It was not found alive in lakes. South of the Canadian Interior Basin it often occurs in streams as narrow as 6 feet or less (Clarke & Berg, 1959: 32). Species usually found associated with *L. compressa* within the research area are *Lampsilis radiata siliquoidea*, *Anodonta grandis* (*s. lat.*), and (west of Ontario) *Lasmigona complanata*.

The anatomy of *Lasmigona compressa* has been discussed by Ortmann (1911: 281). The species is normally hermaphroditic and males are very rare. In Pennsylvania the breeding season lasts from August to the following June. The specimens from the Canadian Interior Basin were all collected between July 2 and August 10 during 4 summers and none were found to be gravid. Glochidia of this species are subtriangular, almost semicircular, with hooks, and measure about 0·34 mm in length and 0·28 mm in height. The host fish is unknown. Hermaphroditism may be an adaptive character for life in headwater streams and for passive introduction into previously unoccupied areas.

Remarks: The taxonomy of this species and the status of *Unio viridis* Rafinesque, 1820, have been the subject of much controversy. Ortmann & Walker (1922: 34) considered the problem and concluded that *U. viridis* is not recognizable. Frierson (1915: 57, 1920: 127, and 1927: 19, 20), however, has insisted that *U. viridis* is clearly recognizable and is a prior name for the species now called *Lasmigona compressa* (Lea). Ortmann & Walker (loc. cit.) did not recognize that Rafinesque's "longeur d'un pouce et demi au plus" (length 1½ inches) refers to the height of the shell and not to the length, even though it is well-known that "length" as used by Say, Barnes, and other early 19th century authors meant height, as now defined. But J. P. E. Morrison has pointed out (pers. comm.) that the other relative dimensions given by Rafinesque are incorrect for *L. compressa* and that the species does not occur in the Kentucky River and in adjacent streams, the type locality given by Rafinesque. See Simpson (1900: 662–3) for further details of synonomy.

Lasmigona compressa appears to have used 2 diffuse routes for invasion of the Canadian Interior Basin, one by way of the upper St. Lawrence River system into some north-flowing river systems in Ontario and the other by way of the upper Mississippi River system into the Red River system and other parts of the Nelson River drainage area.

Lasmigona complanata (Barnes)
White Heel-Splitter;
Plate 4, Figs. 5, 6; Map 7.

Alasmodonta complanata Barnes, 1823: *Amer. J. Sci.*, *6*: 278, pl. 13: 21, Type locality: "Fox River" and "Wisconsin."

Unio katherinae Lea, 1838: Synopsis of the Genus Unio, p 35; 1839: *Trans. Amer. phil. Soc.*, *6*: 143. Type locality: "Lake Superior."

Diagnosis: Shell moderately large, ovate relatively compressed, with a well-developed dorsal projection, thick pseudocardinal hinge teeth, rudimentary lateral teeth, and white nacre.

Description: Shell medium to large (up to about 7½ inches long), ovate, subtruncate posteriorly, thickened anteriorly, and with a distinct dorsal projection or wing, especially in young specimens. Periostracum brownish, lighter and indistinctly rayed in many young specimens, and roughened by lines of growth. Dorsal projection compressed and high in young specimens, unsculptured, except by lines of growth (in specimens from the Canadian Interior Basin), and less prominent to absent in older specimens. Beaks narrow, not inflated, slightly elevated, and well-sculptured with double-looped ridges. In some specimens the loops are elevated and pustulous (Pl. 15, Fig. 7). Pseudocardinal teeth large, thick, variable and irregular, 1 on the right valve and 2 on the left. In some specimens 1 or 2 small additional pseudocardinal teeth are present on the right valve on either side of the major tooth. Interdental projection in the left valve articulating with a corresponding groove in the right valve. In some specimens the interdental projection is not developed. Lateral teeth absent or obsolete. Nacre white and tinged with bluish-white posteriorly.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Red River, Abercrombie, N.D.					
L, mm	7	127·2 —183·5	157·0	—	—
H/L	7	0·645— 0·772	0·699	0·017	0·045
W/L	7	0·283— 0·398	0·337	0·031	0·084
Whitemouth River, Whitemouth, Man.					
L, mm	10	72·2 — 90·2	83·3	—	—
H/L	10	0·678— 0·758	0·719	0·009	0·027
W/L	10	0·263— 0·323	0·288	0·006	0·019
Swan River, 8 mi N of Norquay, Sask.					
L, mm	21	51·4 —134·1	99·5	—	—
H/L	21	0·643— 0·804	0·704	0·008	0·038
W/L	21	0·258— 0·401	0·320	0·007	0·034

Feature	N	Range	Mean	S.E.$_M$	S.D.
Shell River, 6 mi W of Prince Albert, Sask.					
L, mm	17	36·9 —115·5	66·1	—	—
H/L	17	0·689— 0·817	0·752	0·008	0·033
W/L	17	0·242— 0·309	0·269	0·005	0·021

Records:

Winnipeg River system. Sturgeon River, Minn. (Dawley, 1947: 679). Lake of the Woods, Ont. Winnipeg River, Minaki, Ont. (both Mozley, 1938: 124). Whitemouth River near Whitemouth, Man. (1951, W. E. Godfrey!; also this survey). Birch River near McMunn, Man. (this survey).

Red River system. Red River: Abercrombie, N.D., near Drayton, N.D. and St. John Baptiste, Man. Sand Hill River, Climax, Minn. Sheyenne River, 1 mi E of Kindred, N.D. (all this survey). Red Lake River, Crookston, Minn. (Univ. Minn.). Otter Tail River, Buffalo River, and Two Rivers, Minn. Maple River, Turtle River, Forest River, Tongue River, and Pembina River, N.D. (all Cvancara, 1967: 189). Little Pine Lake outlet, Minn.; West Lost Lake outlet, Minn.; and Otter Tail River, Perham, Minn. (all Wilson & Danglade, 1914: 12). Roseau River, 8 mi N of Tolstoi, Man. Rat River, 1 1/2 mi S of La Rochelle, Man. Seine River, Grande Pointe, Man. (all this survey). Assiniboine River, 3 mi NE of Amsterdam, Sask. (this survey); Millwood, Man. (1888, J. B. Tyrrell!); 12 mi NW of St. Francis Xavier, Man.; and Winnipeg, Man. city limits (both this survey). Qu'Appelle River, 11 mi N of Whitewood, Sask. Shell River, 6 mi E, 8 mi E, and 9 mi NNE of Roblin, Man. Minnedosa River: 11 mi NNE of Elphinstone, Man. and 10 mi NNW of Minnedosa, Man. (all this survey). Souris River, Souris, Man. (1882, A. R. C. Selwyn!).

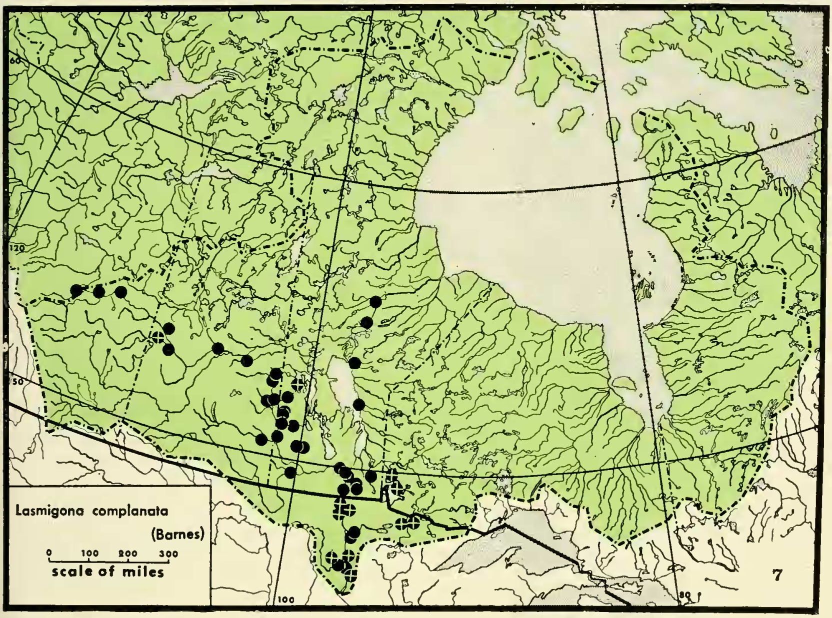
Lake Winnipegosis drainage area. Shoal River (Mozley, 1938: 124). Valley River, Grandview, Man. Woody River, 8 mi N of Swan River, Man. Swan River, 8 mi N of Norquay, Sask. Fir River, 3 mi S of Hudson Bay, Sask. Red Deer River, 4 mi S of Hudson Bay, Sask. (all this survey).

Saskatchewan River system. Lower Saskatchewan River (Mozley, 1938: 124). Carrot River, N E of Arborfield, Sask. (1935, R. T. D. Wickenden!) Shell River, 6 mi W of Prince Albert, Sask. (this survey) Battle River and " Battle River Lake ",Sask.(Mozley, 1938: 124). Tributary of Battle River, 1 mi S of Battleford, Sask. (1964, E. L. Bousfield!). Turtlelake River, Edam, Sask. (this survey). Battle River " 3 mi above Grattan Lake ", Alta. (1885, J. B. Tyrrell!). Sturgeon River, 3 mi N of Villeneuve. Alta. and White Earth Creek, 4 mi NE of Smoky Lake, Alta. (both this survey).

Nelson River drainage area. Lake Winnipeg (Mozley, 1938: 124). Pigeon River, Man. and Gunisao River, Man. (both 1895, J. B. Tyrrell!). Nelson River at 50°15′N, 97°W (1906, O. O'Sullivan!) and Nelson River, unspecified locality (1878, R. Bell!) Burntwood River, Man. (1906, W. McInnes!).

Distribution: Ohio-Mississippi River system from Ohio and Pennsylvania west to Minnesota and Iowa and south to Oklahoma and Louisiana. Alabama River drainage, Ala. Upper St. Lawrence River system in Lake Superior, Lake Huron, and some southern tributaries of Lake Michigan and Lake Erie. Widely distributed in the Lake Winnipeg-Nelson River drainage area from western Ontario to Alberta.

Biology and Ecology: During this survey *Lasmigona complanata* was found only in rivers from 25 to 200 feet wide. The current at all these localities was slow, moderate, or rapid and the vegetation was generally sparse at most



localities, but more abundant in some. The bottom was invariably sand or mud, with or without gravel and rocks. At localities in the Red River and its vicinity this species was usually a minor element of the unionid faunae found. At localities west of that region it was relatively more common and ordinarily ranked second or third in abundance behind *Lampsilis radiata siliquoidea* or *Anodonta grandis* or both.

The anatomy of *Lasmigona complanata* has been discussed by Ortmann (1912: 282) and by Baker (1928a: 149). The breeding season in Pennsylvania lasts at least from mid-September to mid-May. The soft parts of all specimens seen were yellowish to orange. Only 1 gravid female was collected and that was found on August 9, 1964 in the Seine River at Grande Pointe, Man. The outer gills of this specimen were greatly swollen with developing eggs about 0·38 mm in diameter, but glochidia had not yet formed. The glochidia are reported to be sub-triangular, with hooks, and have been measured as 0·28×0·30 mm to 0·34×0·34 mm (Ortmann, 1919: 134). The host fish is unknown.

Remarks: Several recent authors, e.g., Frierson, 1927; Baker, 1928b; and La Rocque, 1953, have used the combination *Lasmigona complanata katherinae* (Lea) (originally proposed for a depauperate specimen supposedly from Lake Superior) for the smaller, northern "subspecies." Such usage, however, is not tenable. Specimens from the Red River reach lengths exceeding 180 mm, but in smaller streams and in otherwise apparently less favourable habitats maximum lengths are much smaller. This relationship can be seen

in a number of species and there is no evidence that it is other than ecophenotypic.

Costation of the dorsal wing has not been used to differentiate subspecies but it is a character that may be significant. No specimens seen from the Canadian Interior Basin are costate although a few examples do possess dorsal wings which are not quite smooth. Many specimens from the Ohio-Mississippi River system are similarly unsculptured although numerous others clearly exhibit some degree of costation. This feature is most extremely developed in specimens from the Black Warrior River in Alabama. These are strongly ribbed and grooved over the whole dorsal and posterior surfaces and appear to be quite distinct.

Tribe Anodontini *s. str.*

Shells thin, fragile in many species, and without sculpturing on the posterior slope. Pseudocardinal teeth vestigial or absent. Lateral teeth entirely absent.

Genus *Anodonta* Lamarck

Anodonta Lamarck, 1799: *Mem. Soc. Hist. nat. Paris*, p 87. Type species: *Mytilus cygneus* Linnaeus, by original designation. The generic name *Anodonta* has been placed on the Official List of Generic Names in Zoology by the International Commission on Zoological Nomenclature (Opinion 94).

Shells uniformly thin or thin posteriorly and thickened anteriorly. Most species are elliptical or ovate but in some species a posterio-dorsal projection or "wing" is well developed. Hinge without teeth in all species and hinge line straight or evenly convex. Beak sculpturing single or double-looped and consisting of 4 or 5 parallel bars or, in some species with single-looped sculpture, of up to 10 or more bars. Marsupia occupying the whole outer gills and, when full, forming smooth, thick, reddish pads.

Simpson (1914) has recognized about 55 world-wide species within this Holarctic genus. Frierson (1927) lists 29 species and subspecies of *Anodonta* from North America alone. Both these totals will probably be substantially reduced by future research. Geologic range: Upper Cretaceous to Recent.

Frierson (1927: 14) has applied the subgenus name *Pyganodon* Crosse & Fischer (1894: 518) to the *Anodonta grandis—A. cataracta—A. implicata* group. Crosse & Fischer based this and several other subgeneric divisions on superficial characters such as general shape and relative elevation of the umbones. Anatomical, reproductive, or other more fundamental differences between *A. cygneus* and the *A. grandis* group have not been shown to exist. In fact there is evidence of gene flow between *Anodonta cataracta fragilis* Lamarck of Newfoundland and vicinity, which appears to be related to *A. cygnea*, and both *A. grandis simpsoniana* and *A. cataracta* (*s. str.*) within their zones of contact (see discussions following; also see Clarke & Rick 1963: 22–26). For these reasons *Pyganodon* is not used here.

Analysis of Variation in Anodonta

Anodonta is ubiquitous and abundant in the Canadian Interior Basin and exhibits extreme variation. Fortunately few names have been applied to populations within the area, but even so a problem existed in determining the proper nomenclatorial and systematic status of the populations encountered. In order to determine which aspects of variation are of taxonomic significance, an objective approach was desirable in which all apparently useful characters were analyzed statistically and compared with ecology and zoogeography. Such analysis might

also lead to generalizations concerning differential selection in contrasting habitats.

The characters which appeared to be potentially revealing and amenable to quantification are given below. All measurements are in mm.

1. Ant. to beak/Length. Anterior to beak is the distance from the anterior end of the shell to the beak or umbo, measured parallel to the long axis of the shell. Length is also measured parallel to the long axis.
2. Pt. to base/Height. Point to base is the distance from the most distal point of the posterior end to the ventral edge of the shell, measured perpendicular to the long axis. Height is the maximum dorsal-ventral dimension measured perpendicular to the long axis.
3. Height/Length. A standard ratio, see above.
4. Width/Length. Width is the maximum width of the shell with both valves appressed measured perpendicular to the plane passing between the 2 valves.
5. Beak sculp. Beak sculpture values are determined by scoring each specimen. Three kinds of beak sculpturing were selected as representing the major variations: (*a*) the single-looped condition where each bar is rounded and curved in a broad U-shape; (*b*) the double-looped condition where each bar is bent roughly into a W-shape with rounded lower apices; and (*c*) the nodulous form of the double-looped condition where the lower apices of each W-shaped bar are elevated and enlarged (nodulous) and other parts of each bar are obsolete. An arbitrary scale of 1 to 4 was used as follows: (1) single-looped, (2) midway between the extreme single-looped and extreme (non-nodulous) double-looped, (3) double-looped and (4) nodulous. Intermediate specimens were given intermediate scores, e.g., 1·5, 3·3, etc.

   It is recognized that such a method is an over-simplification. Scoring does not distinguish between specimens which (*a*) have faintly-developed beak sculpturing and those in which the bars are heavy; or (*b*) have beak sculpturing which is composed of a few bars near the umbonal apex and those in which the bars extend far out on the disc. It also fails to identify specimens with combinations of single loops and nodules. Such aberrations *are* recorded in notes, however, and in general the scoring method does provide a convenient and, apparently, a realistic method of comparing populations.
6. Periost. colour (percentage of Green). The number of specimens in each lot which have a partly or wholly green periostracum (i.e., with YG or G scores derived by the use of the standards described below) expressed as a percentage of the entire population sample.
7. Periost. colour (Dk.). Darkness of periostracum colouring, also as determined by scoring with the use of standards, as follows: the palest and yellowest specimen found and the palest and greenest specimen were selected as standards and given values of Y-1 and G-1 respectively. A brown specimen was also selected and given a value of 2. These standards exhibited colours which are approximately equivalent to the following respective values on the Munsell (1929–60) scale: 5Y7/6, 5GY4/4, and 7·5YR4/4. Black was given a value of 3. All specimens were then scored for colour and

PLATE 1. *Fusconaia*, *Quadrula* and *Amblema*

FIGS. 1, 2. *Fusconaia flava*, Assiniboine River near St. Francis Xavier, Manitoba (NMC 14613, 77 mm), ... p 28.

FIGS. 3, 4. *Quadrula quadrula*, Red River, St. John Baptiste, Manitoba (NMC 14607, 83 mm), ... p 32.

FIGS. 5, 6. *Amblema plicata*, Assiniboine River, Winnipeg, Manitoba (NMC 14612, 85 mm), ... p 35.

PLATE 1

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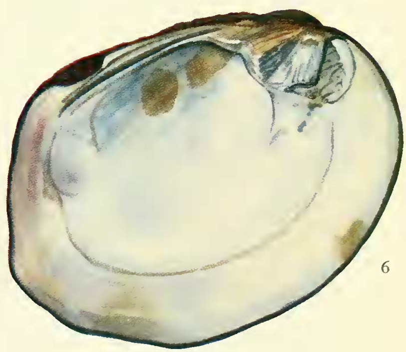

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PLATE 2. *Amblema plicata*

FIGS. 1, 2. Assiniboine River, Winnipeg, Manitoba (NMC 14610, 120 mm). . . . . p 35.

PLATE 2

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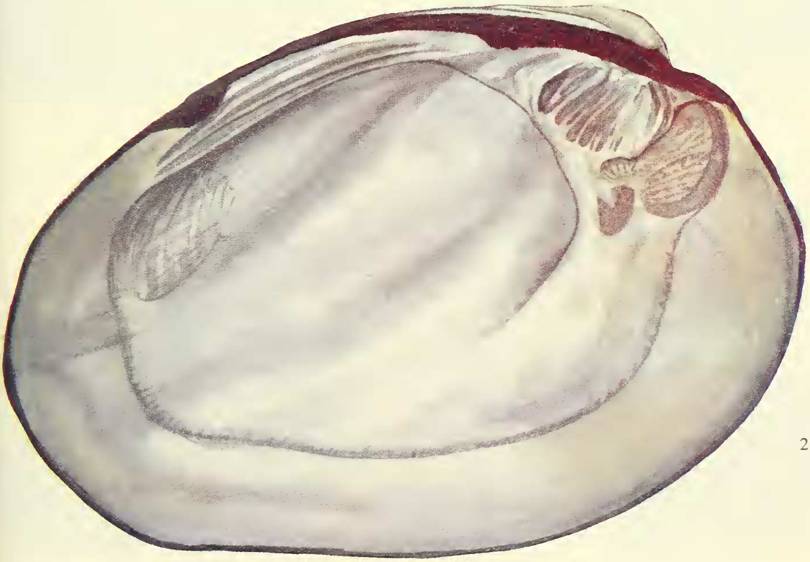

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PLATE 3. *Elliptio complanata*

FIGS. 1–6. Lac Dubuisson near Val d'Or, Quebec (NMC 14602). . . . . p 38.
(FIGS. 1, 2: 61 mm; 3, 4: 70 mm; 5, 6: 57 mm).

PLATE 3

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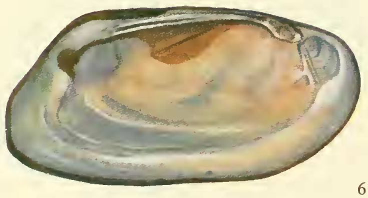

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PLATE 4. *Lasmigona*

FIGS. 1, 2. *Lasmigona compressa*, Fir River near Hudson Bay, Saskatchewan (NMC 14634, 58 mm) . . . . p 44.

FIGS. 3, 4. *Lasmigona costata*, Birtch River near McMunn, Manitoba (NMC 14616, 125 mm) . . . . p 41.

FIGS. 5, 6. *Lasmigona complanata*, Red Deer River near Hudson Bay, Saskatchewan (NMC 14605, 82 mm) . . , ... p 46.

PLATE 4

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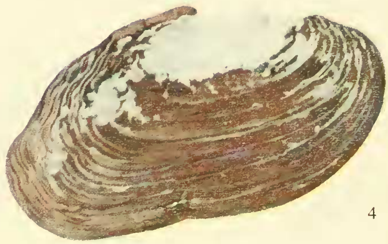

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PLATE 5. *Anodonta grandis*

FIGS. 1, 2. *Anodonta grandis grandis*, Lake Winnipeg near Gimli, Manitoba (NMC 14615, 75 mm) . . . . p 81.

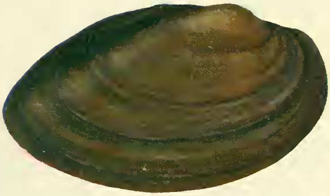
FIGS. 3, 4. *Anodonta grandis grandis*, Wabaskang Lake, 40 mi N of Vermilion Bay, Ontario (NMC 14617, 59 mm) . . . . p 81.

FIGS. 5, 6. *Anondonta grandis simpsoniana*, Wilson Lake near Nellie Lake, Ontario (NMC 14061, 108 mm) . . . . p 85.

FIGS. 7, 8. *Anondonta grandis simpsoniana*, Wilson Lake near Nellie Lake, Ontario (NMC 14601, 64 mm) . . . . p 85.

FIGS. 9, 10. *Anodonta grandis simpsoniana*, Crow River, Central Patricia, Ontario (NMC 14604, 68 mm) . . . . p 85.

PLATE 5



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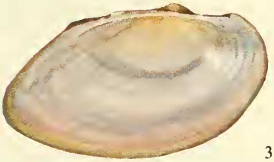

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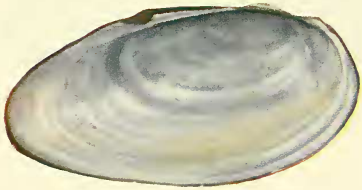

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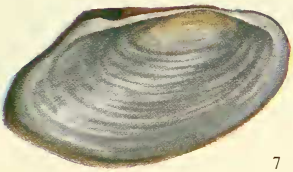

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PLATE 6. *Anodonta, Anodontoides* and *Strophitus*

FIGS. 1–4. *Anodonta kennerlyi*, Crimson Lake near Rocky Mountain House, Alberta (NMC 20727, 84 and 83 mm, respectively) . . . . p 90.

FIGS. 5, 6. *Anodontoides ferussacianus*, Buffalo River near Stockwood, Minnesota (NMC 47506, 57 mm) . . . . p 92.

FIGS. 7, 8. *Strophitus undulatus*, Swan River near Norquay, Saskatchewan (NMC 14620, 67 mm) . . . . p 95.

PLATE 6

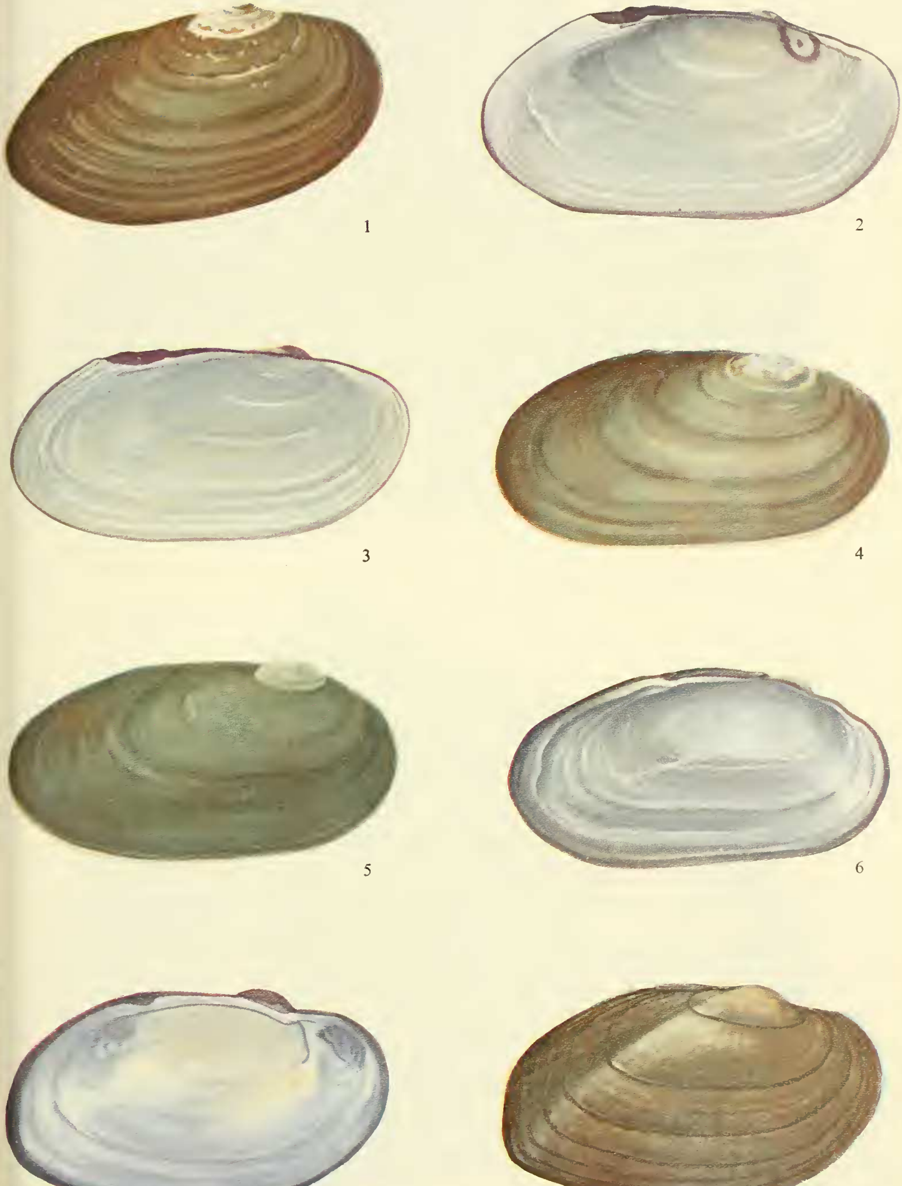

PLATE 7. *Proptera alata*

FIGS. 1, 2. Red River, St. John Baptiste, Manitoba (NMC 39266, 86 mm) . . . . p 99.

PLATE 7

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PLATE 8. *Ligumia recta*

FIGS. 1–4. Assiniboine River, Winnipeg, Manitoba (NMC 14609; figs. 1, 2, male, 112 mm; figs. 3, 4, female, 106 mm) . . . . p 102.

Plate 8

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for darkness, e.g., Y-1·5 (intermediate between Y-1 and 2); YG-1 (intermediate between Y-1 and G-1); 2·5 (darker than the brown standard (2) but not black), etc. For tabulation of results under Periost. colour (Dk.) the degree of darkness was calculated from only the numerical scores without reference to Y or G.

8. Rays. Development of periostracal rays scored on the following scale: 1, rays absent; 2, rays present but weak; and 3, rays strongly developed.
9. Nacre Colour. This was also determined by scoring, as follows: 1, white nacre; 2, nacre faintly bluish; and 3, nacre bluish.

In addition to these characters, other measurements were considered or attempted and for various reasons were judged to be unsatisfactory. Soft part anatomy was examined but since very few specimens were found which were gravid (collecting was done only during the period from June to September) and non-gravid specimens did not exhibit differences which appeared to be significant, detailed anatomical work was not attempted. This decision was also influenced by the statements of Baker (1928b: 156–168) who was unable to detect soft-part differences between the species of *Anodonta*. Of course much additional work needs to be done on the comparative anatomy of *Anodonta*.

An attempt was also made to count growth annuli on the specimens collected. It was impossible to decide whether some of the lines represented annual events or not, however, and the value of the results obtained (after examining hundreds of specimens) was therefore considered minimal. In addition, growth within neighbouring populations may be quite different apparently because of variations in habitat suitability and food supply, and it became obvious that attempts to correlate growth with isotherms or with geography would be unrewarding. The only geographical relationship which emerged is that in extreme northern, peripheral populations growth appears to be very slow and the maximum size reached is much less than in many more southerly populations.

Thirty population samples were selected for statistical analysis (Table 4). These were from stations spread as broadly as possible from west to east across the whole Canadian Interior Basin and represented all *Anodonta* habitats seen. For analysis, preference was given to lots containing 30 or more specimens although in a few cases smaller lots were used to make the geographical and ecological coverage more complete. Three samples from northern peripheral localities were also measured. These could not be inserted into the west-to-east sequence, as below and on charts 1–9, and are reported only on Chart 10 and in the text under *Anodonta grandis simpsoniana*.

The origins of the population samples measured and fully charted are listed below, together with the range and mean values of length (L) and the number of specimens (N) measured for length. The additional measurements taken from these samples are shown on Charts 1–9.

Inspection of Charts 1 to 9 shows that several correlations exist. These appear to be ecological in some cases and geographical in others.

Ecological Correlations

Characters which exhibit good correlations with ecology are: (*a*) relative position of the umbones (Ant. to beak/Length) and (*b*) percentage of the specimens that are partly or wholly green or greenish in periostracal colour (Periost. colour (percentage of Green)). Fairly well-marked correlations with ecology also exist with (*c*) periostracal darkness

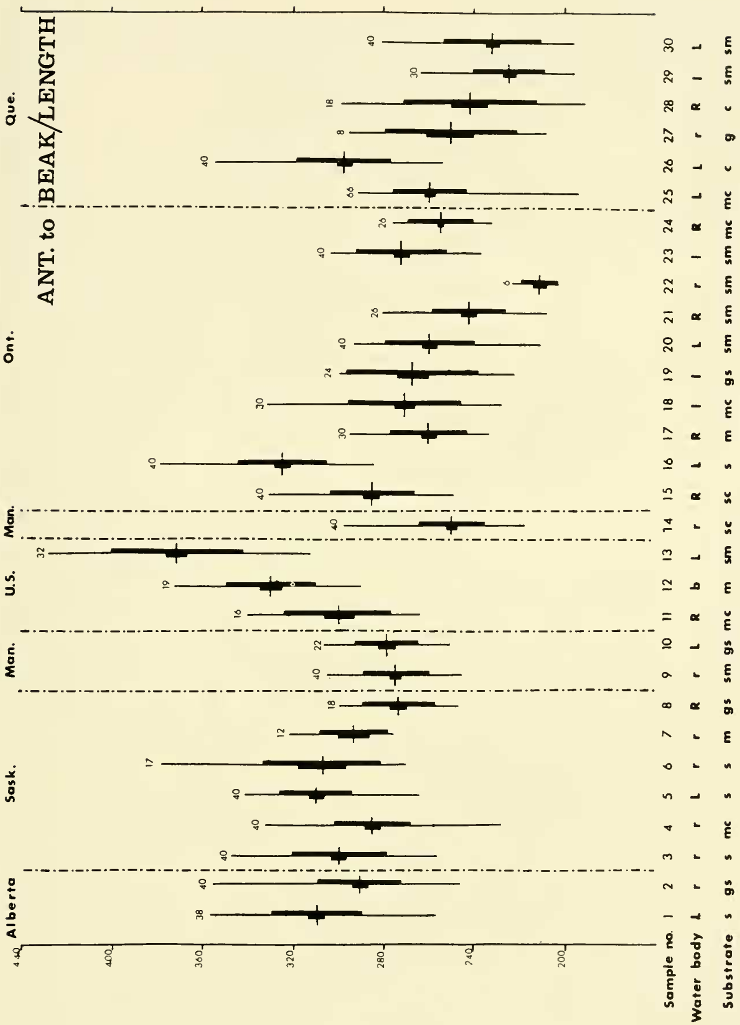


CHART 1. *Anodonta* populations. For explanation see p 51. Ecological symbols used in this and other charts are: b, backwater or impounded portion of a river; c, clay; g, gravel; L, large lake (500 acres or more); l, small lake (less than 500 acres); m, mud; R, large river (100 feet wide or more); r, small river (less than 100 feet wide); s, sand.

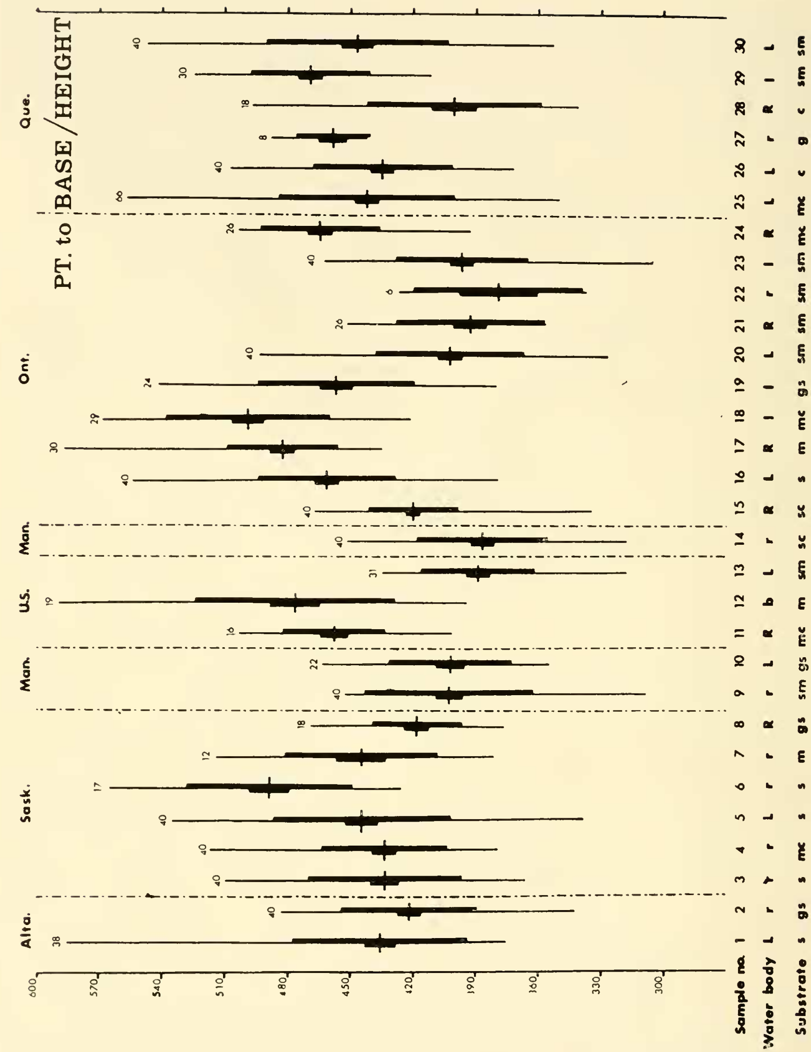


CHART 2. *Anodonta* populations. For explanation see p 51. Symbols are defined in caption for Chart 1.

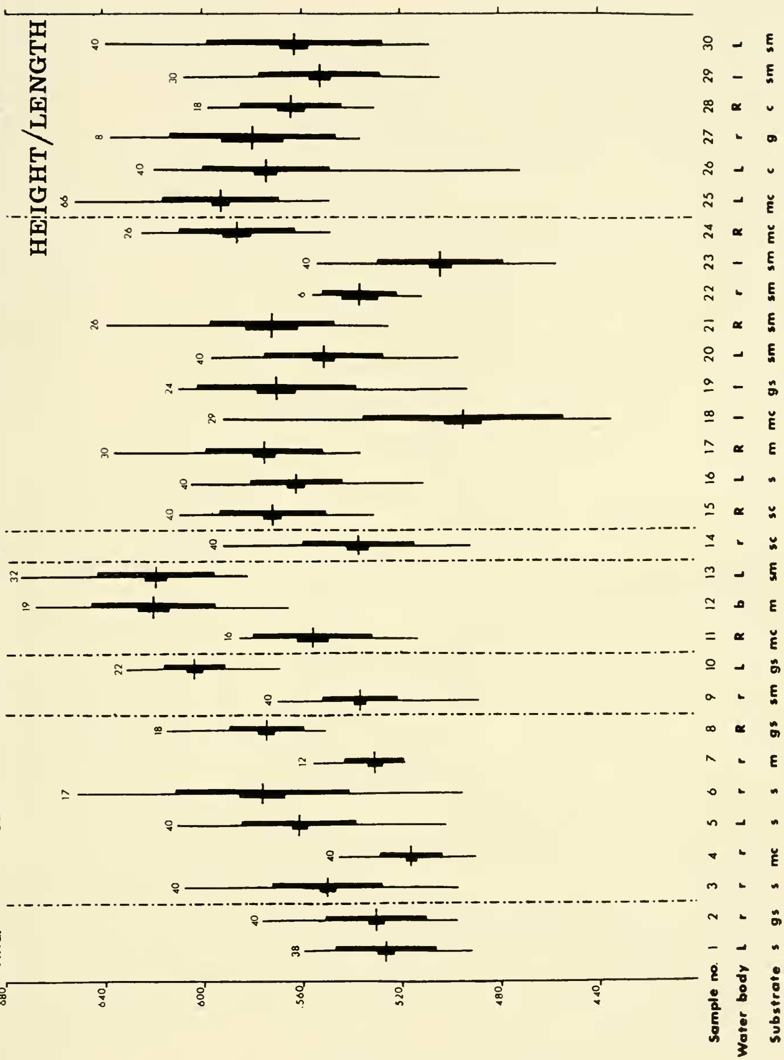


CHART 3. *Anodonta* populations. For explanation see p 51. Symbols are defined in caption for Chart 1.

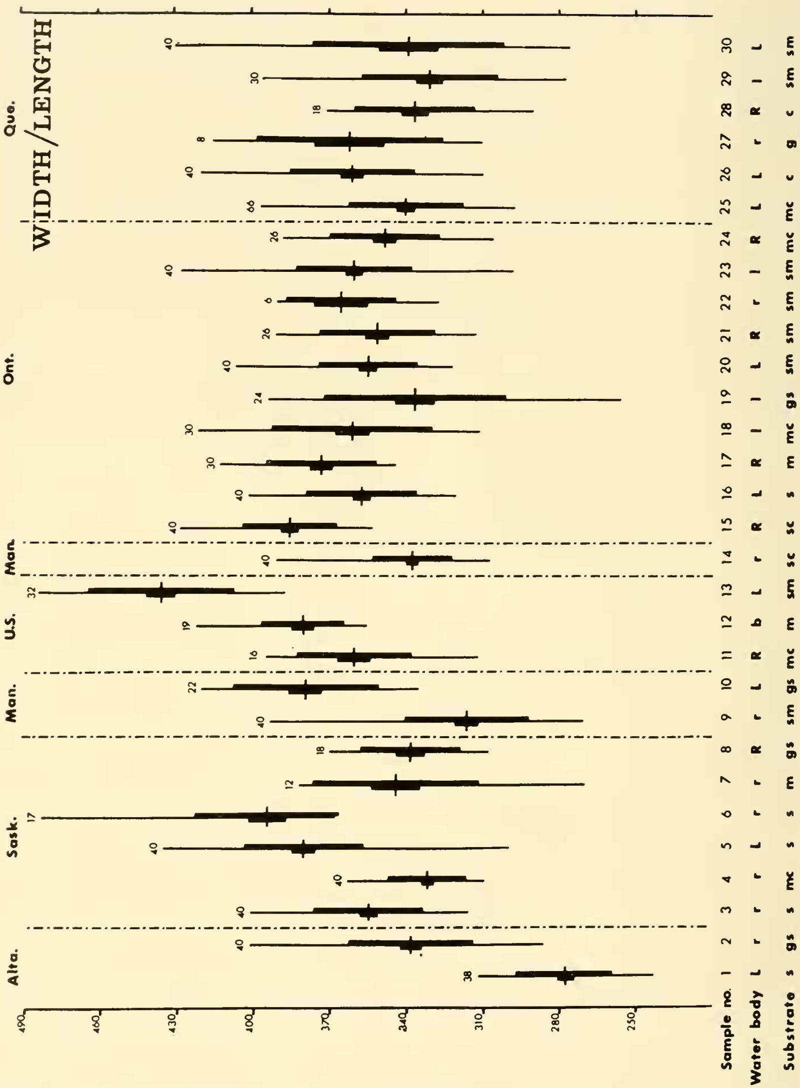


CHART 4. *Anodonta* populations. For explanation see p 51. Symbols are defined in caption for Chart 1.

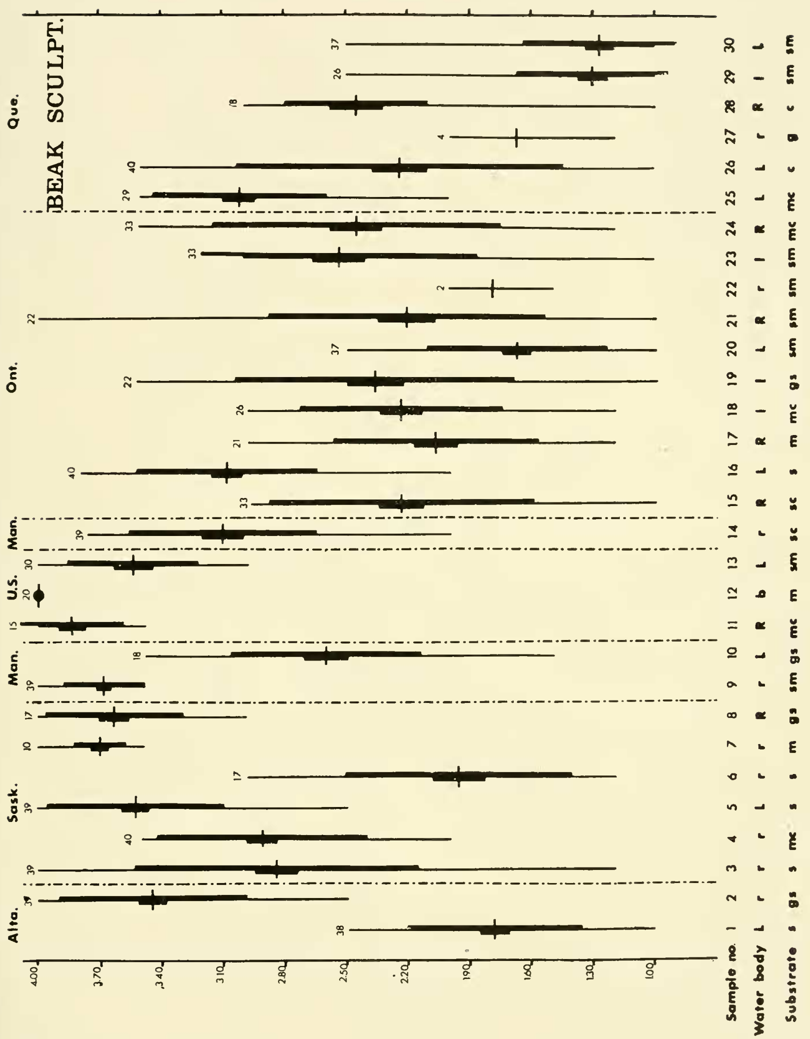


CHART 5. *Anodonta* populations. For explanation see p 51. Symbols are defined in caption for Chart 1.

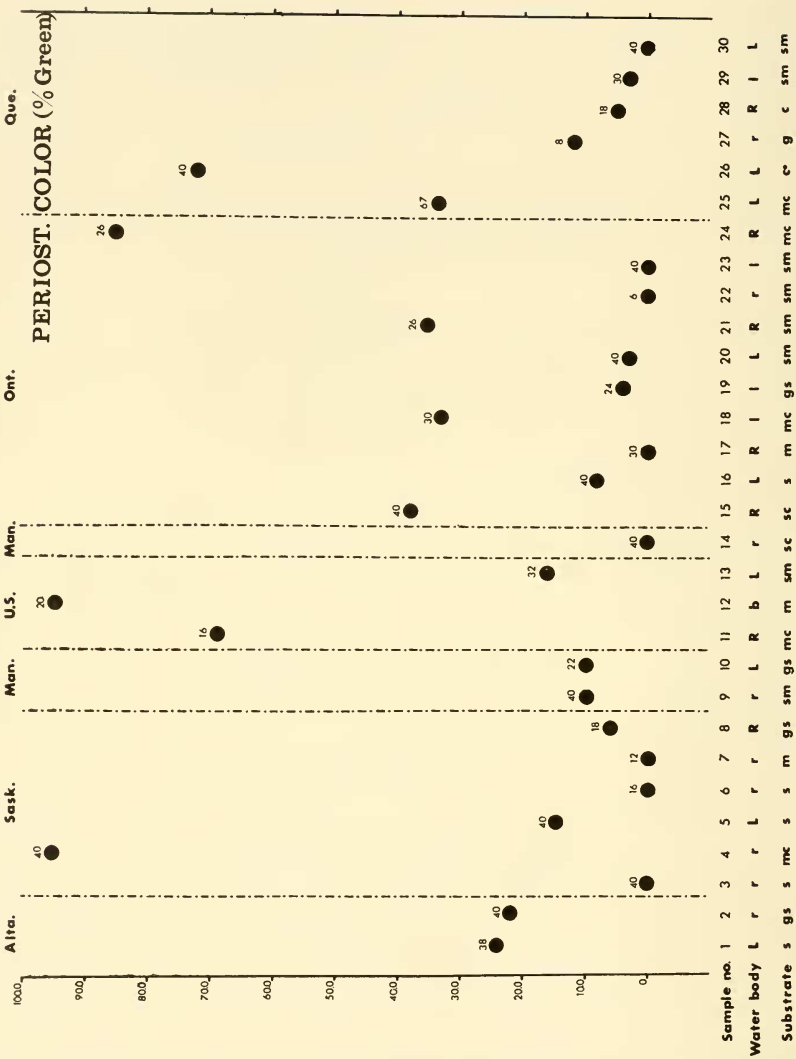


CHART 6. *Anodonta* populations. For explanation see p 51. Symbols are defined in caption for Chart 1.

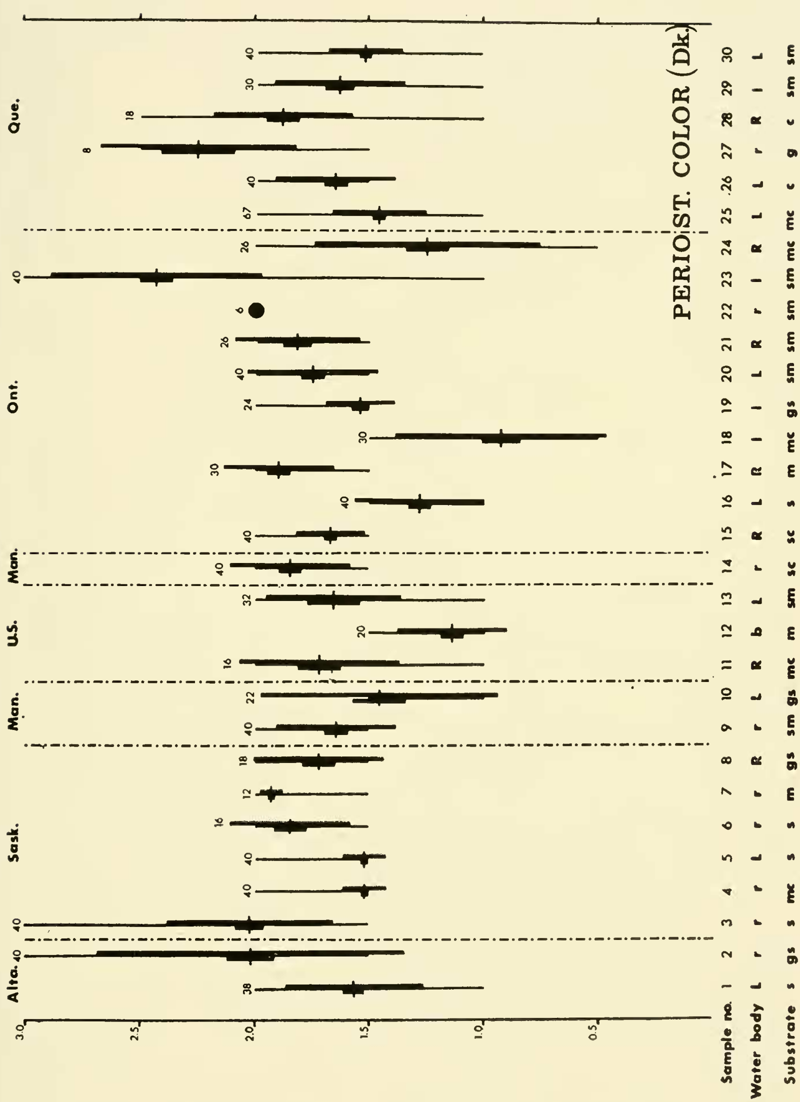


CHART 7. *Anodonta* populations. For explanation see p 51. Symbols are defined in caption for Chart 1.

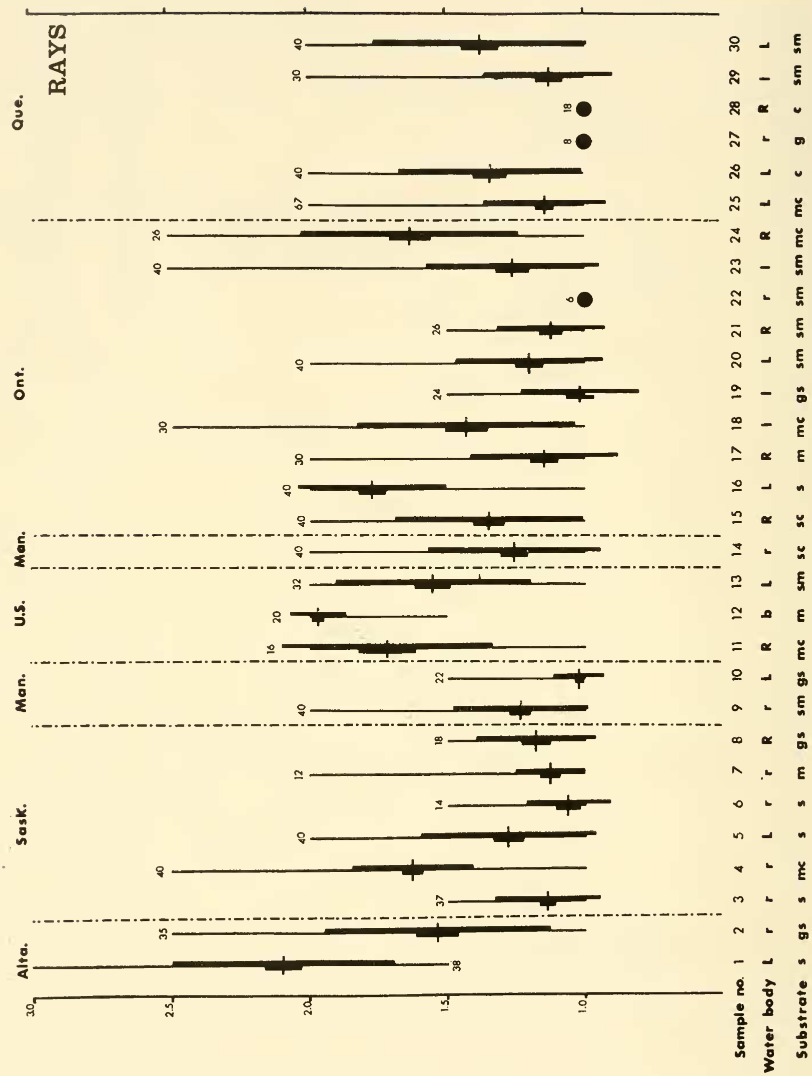


CHART 8. *Anodonta* populations. For explanation see p 68. Symbols are defined in caption for Chart 1,

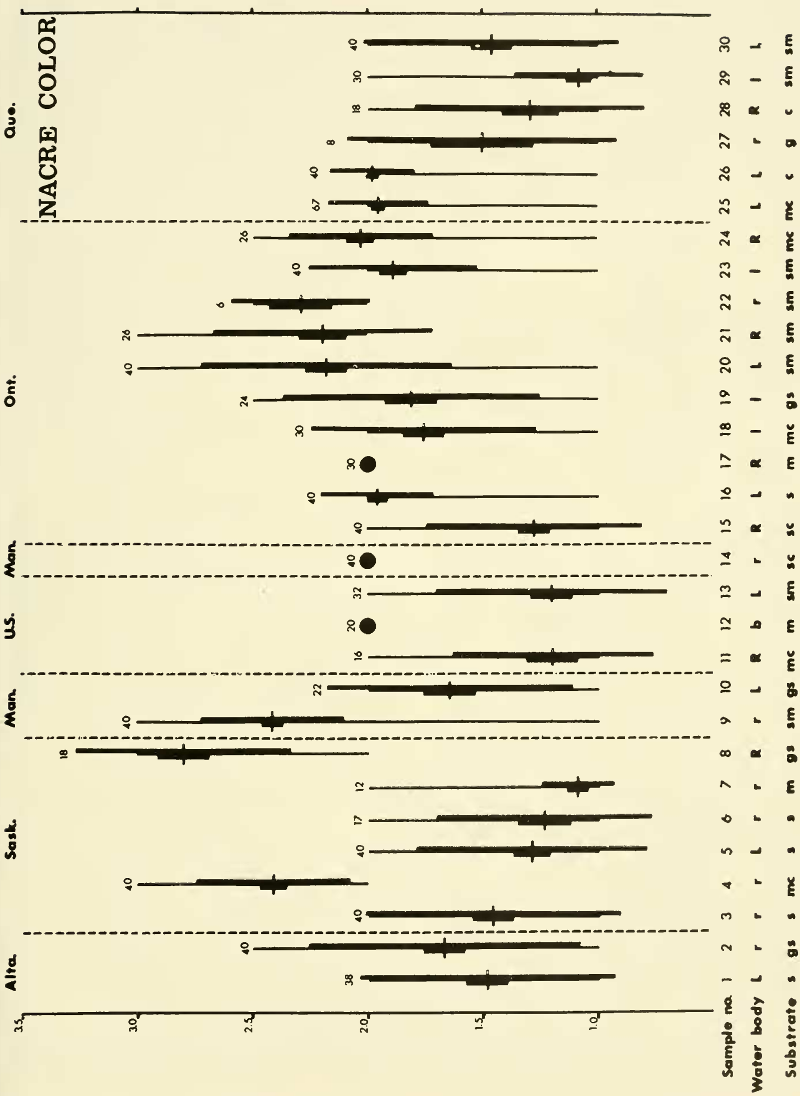


CHART 9. *Anodonta* populations. For explanation see p 68. Symbols are defined in caption for Chart 1.

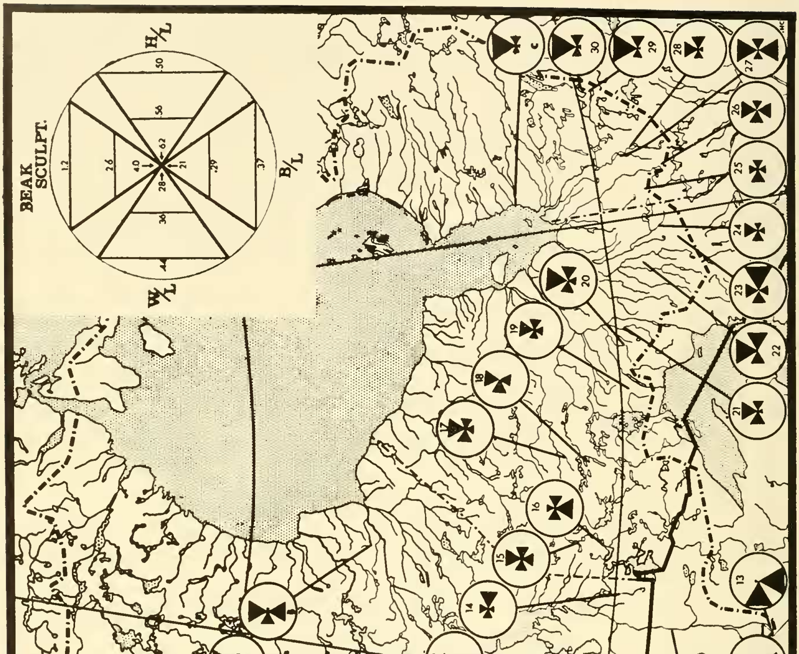


CHART 10. *Anodonta* populations. For explanation see p 81.

TABLE 4. *Anodonta* Populations Analyzed Statistically.

Sample	Locality	Length, mm Min. (Mean) Max.	N
1	Crimson Lake, 9 mi N of Rocky Mountain House, Alta.	45·0—(79·0)— 87·3	38
2	White Earth Creek, 4 mi NE of Smoky Lake, Alta.	51·8—(77·0)—112·5	40
3	Englishman River, 3 mi NW of Spruce Lake, Sask.	64·3—(79·3)— 98·3	40
4	Swift Current Creek, 3 mi N of Waldeck, Sask.	82·3—(95·6)—112·6	40
5	Montreal Lake, 16 mi N of Waskesiu Lake, Sask.	48·0—(61·9)— 82·8	40
6	Qu'Appelle River, Pasqua Lake outlet, near Fort Qu'Appelle, Sask.	34·4—(74·8)—111·9	17
7	Antler Creek, 4 mi W of Carievale, Sask.	55·0—(101·5)—131·8	12
8	Red Deer River, 4 mi S of Hudson Bay, Sask.	42·3—(63·0)— 79·0	18
9	Shell River, 8 mi E of Roblin, Man.	66·7—(75·7)—110·0	40
10	North shore of Clear Lake, 8 mi W of Wasagaming, Man.	43·0—(60·5)— 78·8	22
11	Red River, Drayton, N.D.	60·2—(114·8)—147·8	16
12	Outlet of Traverse Lake, 18 mi N of Brown's Valley, Minn.	81·0—(93·8)—103·0	19
13	Traverse Lake, Brown's Valley, Minn.	66·0—(86·4)—107·5	32
14	Whitemouth River, Whitemouth, Man.	60·8—(67·6)— 75·8	40
15	Chukuni River, 2 mi E of Red Lake, Ont.	52·7—(68·1)— 82·0	40
16	Wabaskang Lake, 40 mi N of Vermilion Bay, Ont.	44·7—(59·2)—105·8	40
17	Crow River, Central Patricia, Ont.	56·0—(66·6)— 72·8	30
18	Unnamed lake, 71 mi N of Savant Lake, Ont.	80·0—(89·3)—110·3	30
19	Wild Goose Lake, 39 mi W of Longlac, Ont.	28·4—(58·5)— 95·6	24
20	Klotz Lake, 30 mi E of Longlac, Ont.	45·0—(70·6)— 86·3	40
21	Shekak River, 34 mi W of Hearst, Ont.	44·4—(53·7)— 65·8	26
22	Departure Creek, 7 mi W of Smooth Rock Falls, Ont.	50·5—(72·1)— 82·0	6
23	Wilson Lake, 25 mi S of Cochrane, Ont.	76·3—(102·3)—116·1	40
24	Black River, Matheson, Ont.	49·7—(66·9)— 95·9	26
25	Macamic Lake, 11 mi E of La Sarre, Que.	31·2—(49·7)— 77·4	66

Sample	Locality	Length, mm Min. (Mean) Max.	N
26	Lac Dubuisson, 5 mi NW of Val d'Or, Que.	50·6—(62·3)— 78·6	40
27	Taschereau River, 40 mi N of Senneterre, Que.	58·0—(66·6)— 87·8	8
28	Bell River, 33 mi N of Senneterre, Que.	39·3—(68·9)— 83·6	18
29	Lake Gilman, Chibougamau, Que.	63·4—(84·1)—113·0	30
30	Caché Lake, 5 mi SW of Chibougamau, Que.	56·6—(75·4)—113·5	40

(Periost. colour (Dk.)) and (*d*) development of periostracal rays (Rays). Relative elevation of the posterior tip as a measure of shape (Pt. to base/Height) showed no correlations whatever. The correlations with ecology are discussed in detail below.

In each province and in that part of the United States investigated, when each region was considered separately (thus minimizing the effects of geographical variation), the highest values of the ratio Ant. to beak/Length were invariably seen in samples from large lake habitats. In most cases the bottoms were of sand. High values of the Ant. to beak/Length ratio indicate umbones which are placed further back, i.e., are more centrally located. Such values also indicate specimens in which the anterior (foot) region is longer or the posterior region is reduced or both. Superior development of the foot is also implied by high values of this ratio.

Of special interest in this connection are the high values of Ant. to beak/Length seen in sample 12. This sample is from a small impounded section of the outlet of Lake Traverse. It occupies an area of about 1/4 acre, has a maximum depth of about 4 feet, and a mud bottom. It is dammed at both ends and also has a fish barrier fence at the downstream end but no such barrier between it and Lake Traverse. The only nearby population of *Anodonta* is in Lake Traverse (see sample 13), the northern end of which is just above the upstream dam. The *Anodonta* population in this backwater is apparently an extension of the lake population and, although the 2 habitats are ecologically quite different, the populations are similar in that both exhibit very high values of Ant. to Beak/Length.

The good correlations of this ratio with ecology strongly suggest that physical selection occurs in many lakes for individuals best able to maintain their positions in exposed habitats and on shifting substrates, i.e., for individuals with large foot volumes. The data from samples 12 and 13 mentioned above, and similar observations of other populations, also suggest that such selection alters in the local gene pool the frequency of genes responsible for the development of the foot and of shell shape.

Greenness of periostracum, i.e., high and low values of Periost. colour (percentage of Green), appears to be correlated with substrate (see Chart 6). Sand bottoms appear to be inimical to greenness and mud bottoms favourable. This agrees with the writer's experience elsewhere that the greenest specimens always oc-

curred on mud bottoms. Ortmann (1919: 140) reports similar observations. Such correlations suggest a positive relationship between periostracal greenness and with concentrations of organic compounds in the substrate.

Darkness of periostracum (Chart 7) appears to be related to kind of habitat and to substrate, but the relationship is not clear-cut. River habitats, with some exceptions, produced the darkest individuals. Likewise lake habitats, and frequently lakes with sand bottoms, produced the palest. However, exceptions to these generalizations occur.

Development of periostracal rays shows some correlation with substrate. Mixed sand-mud substrates appear to be unfavourable to the development of rays but specimens collected from sand or mud alone were often quite strongly rayed. Rays appear to depend in part on greenness (which is positively correlated with mud) and on paleness of colour (which is positively correlated with sand), but many exceptions occur.

Geographical Correlations

Characters that exhibit well-marked correlations with geography are: (a) beak sculpturing, (b) relative position of the umbones (Ant. to beak/Length) and (c) relative obesity (Width/Length). A fairly good correlation between (d) relative height (Height/Length) and geography also appears to exist, and some correlation of (e) nacre colour and geography is also suggested. Chart 10 presents a comparison of mean values for characters which are most clearly related to geography, i.e., characters, a, b, c, and d (above). Such an arrangement provides a diagrammatic, visual comparison of the degree of character concordance which exists.

Even though much inter-population variation is evident and the amount of concordance shown by the 4 characters over large parts of the region is not at all complete, the concordance which is observed is considered sufficient for the recognition of 2 subspecies, *Anodonta grandis grandis* and *Anodonta grandis simpsoniana*, and of a separate species, *Anodonta kennerlyi* Lea. These taxa are discussed in detail below under their respective headings.

Anodonta grandis grandis Say

Floater Mussel;
Plate 5, Figs. 1-4; Map 8.

Anodonta grandis Say, 1829: *N. Harmony Dissem. useful Knowl.*, *2*: 341 (Binney reprint, 1858: 139). Type locality: "Fox River of the Wabash."

Anodonta kennicottii Lea, 1861 (in part): *Proc. Acad. natr. Sci. Philad.*, *5*: 56; 1862: *J. Acad. natr. Sci. Philad.*, *5*: 214, pl. 33: 283. Type locality: "Great Slave Lake at Fort Rae and north end of Lake Winnipeg, Arctic America." See discussion under *A. g. simpsoniana*.

Anodonta dallasiana Lea, 1863: *Proc. Acad. natr. Sci. Philad.*, *7*: 190; 1866: *J. Acad. natr. Sci. Philad.*, *6*: 29, pl. 11: 28. Type locality: "Lake Winnipeg, at the mouth of the Saskatchewan River." This appears to be intermediate between *A. g. grandis* and *A. g. simpsoniana* Lea.

Diagnosis: Shell medium-sized to large, ovate, thin, fragile, without hinge teeth, periostracum brownish or greenish, and with double-looped beak sculpturing which in most specimens is also tuberculous.

Description: Shell medium-sized to large (up to about 6 inches long), inflated, ovate, thin to slightly thickened, fragile (usually cracking extensively on drying), and unsculptured except for lines of growth and beak sculpture. Posterior slope compressed dorsally and somewhat alate in young specimens. Periostracum yellowish-brown, greenish, greenish-brown, or blackish. Many specimens are extensively but obscurely rayed and exhibit concentric darker and lighter bands. Beaks subinflated

and projecting well above hinge line. Beak sculpture distinct in most specimens and variable but ordinarily double-looped, tuberculous, and rather heavy (see text Fig. 4, p 90). Hinge teeth absent but hinge plate distinct, straight dorsally, and slightly thickened. Nacre white or bluish white, rarely pinkish.

Measurements

For measurements see charts 1–10, samples 2 to 14 and 16, under Genus *Anodonta*.

Records*

Albany River system. Small lake, Rupert Township, 8 mi W of Nakina, Ont. (this survey).

Winnipeg River system. Lake of the Woods (1884, J. B. Tyrrell!). Red Lake, Cochenour, Ont. Wabaskang Lake, 40 mi N of Vermilion Bay Ont. Vermilion Lake, Vermilion Bay, Ont. (all this survey). Rennie River, Rennie, Man. (1964, F. R. and J. C. Cook!). Birch River, near McMunn, Man. Whitemouth River, Whitemouth, Man. Winnipeg River, 3 mi E of Fort Alexander, Man. (all this survey).

Red River system. Traverse Lake, Brown's Valley, Minn. Outlet of Traverse Lake, 18 mi N of Brown's Valley, Minn. Bois de Sioux River, 2 mi E of Fairmount, N.D. Red River: Abercrombie, N.D.; 3 mi W of Nielsville, Minn.; 2 mi NE of Drayton, N.D.; and St. John Baptiste, Man. Mustinka River, 1 mi W of Wheaton, Minn. Wild Rice River, 9 mi SW of Wahpeton, N.D. Sheyenne River, 1 mi E of Kindred, N.D. Sand Hill River, Climax, Minn. Seine River, Grande Pointe, Man. Antler Creek, 4 mi W of Carievale, Sask. Souris River [Mouse River], 15 mi WNW of Mohall, N.D. Souris River tributary, 2 mi S of Weyburn, Sask. Assiniboine River: 2 mi NE of Amsterdam, Sask. and western city limits of Winnipeg, Man. Whitesand River 9 mi ESE of Sheho, Sask. Qu'Appelle River: outlet of Pasqua Lake, Echo Valley Provincial Park, Sask.; 4 mi W of Welby, Sask.; and 11 mi N of Whitewood, Sask. Clear Lake 4 mi and 8 mi N of Wasagaming, Man. Minnedosa River: 10 mi NNW of Minnedosa, Man. and 11 mi NNE of Elphinstone, Man. Shell River: 9 mi NNE, 6 mi ESE, and 8 mi E of Roblin, Man. (all this survey).

Lake Winnipegosis drainage area. Willow Bend Creek, 4 mi NNE of Westbourne, Man. Ebb and Flow Lake, 4 mi NNW of Kinosota, Man. Valley River, Grandview, Man. Swan River, 8 mi N of Norquay, Sask. Woody River, 8 mi N of Swan River, Man. Fir River, 3 mi S of Hudson Bay, Sask. Red Deer River, 4 mi S of Hudson Bay, Sask. (all this survey).

Saskatchewan River system. Swift Current Creek, 3 mi N of Waldeck, Sask. Sturgeon River, 3 mi N of Villeneuve, Alta. White Earth Creek, 4 mi NE of Smoky Lake, Alta. (all this survey). Vermilion River near Mannville, Alta. (1886, J. B. Tyrell and D. B. Dowling!). Battle River, 1 mi S of Battleford, Sask. (1964, E. L. Bousfield!). Englishman River, 3 mi NW of Spruce Lake, Sask. Turtlelake River: Turtleford and Edam, Sask. Shell River, 6 mi W of Prince Albert, Sask. Mystik Creek, 30 mi S of Flin Flon, Man. (all this survey).

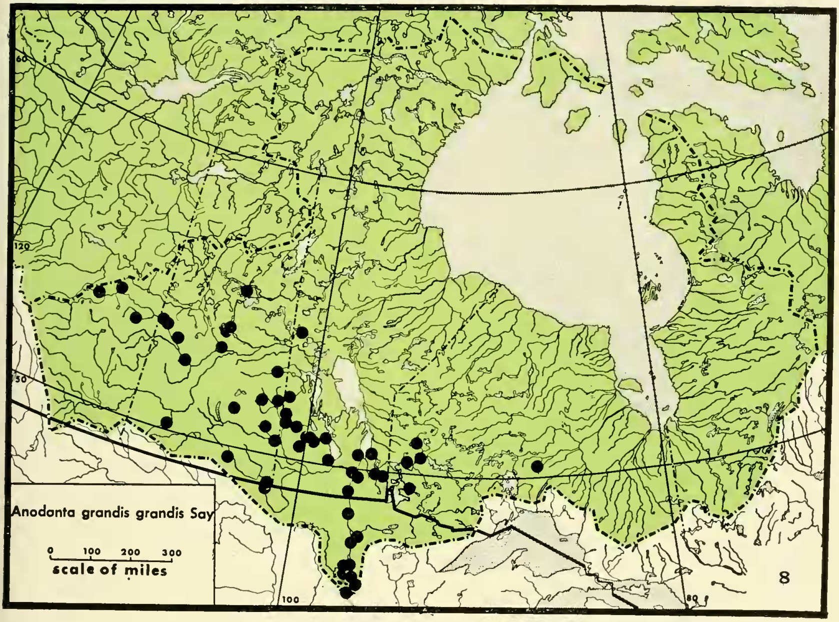
Nelson River system. Lake Winnipeg, southwest corner, 20 mi S of Gimli, Man. (this survey).

Churchill River system. Bittern Creek, 15 mi N of Waskesiu, Sask. Montreal Lake, 16 mi N of Waskesiu, Sask. Midway Lake, 12 mi N of La Ronge, Sask. (all this survey).

Distribution: Mississippi-Missouri River drainage; Gulf of Mexico drainage area in Louisiana and Texas; most of the St. Lawrence River drainage and the Canadian Interior Basin from western Ontario to Alberta. Precise geographical limits of *A. grandis* (*s. str.*) at the edges of its range remain to be worked out.

Biology and Ecology: In the region covered by this report *Anodonta grandis grandis* occurred in medium-sized and large lakes and in rivers ranging from 20 feet (Wild Rice River, 9 mi SW of Wahpeton, N. D.) to 300 feet (Souris River, 15 mi WNW of Mohall, N. D.) in width. Bottoms were of all types (see charts 1–9) and the density of

* Because of uncertainties regarding subspecies identifications reported in the literature only specimens examined are listed.



aquatic vegetation varied from thick to absent, although in 89% of the localities it was moderately dense or sparse. The most commonly associated species was *Lampsilis radiata siliquoidea*. It occurred at 32 of the 56 localities at which *A. grandis* (*s. str.*) was collected during this survey.

The anatomy and reproduction of *Anodonta grandis* are described by Ortmann (1911: 292). Monoecious and dioecious individuals occur (van der Schalie & Locke, 1941). In Pennsylvania the breeding season lasts from early August to the following April or May. Only 2 gravid specimens with glochidia were collected during this survey, both from the Red River at St. John Baptiste, Man., on August 12, 1961. The glochidia were fully formed, triangular-ovate in shape, and varied in size from 0·36 mm long and 0·33 mm high to 0·31 × 0·28 mm. On August 3, 1964 and on August 22, 1961, gravid specimens with eggs were collected at Sheyenne River, 1 mi E of Kindred, N. D. and at Wabaskang Lake, 40 mi N of Vermilion Bay, Ont., respectively. (The Wabaskang Lake population is intermediate between *A. g. grandis* and *A. g. simpsoniana* but is considered to be closer to the former.) The marsupia in all 3 lots occupied the whole of the outer gills as thick pads. The pads were pale and firm in the specimens containing eggs but reddish-brown and fragile in those with mature glochidia.

Fish hosts of *Anodonta grandis* are reported by Lefevre & Curtis (1912: 163) and Morrison (in Clarke & Berg, 1959: 38) as follows:

Golden shiner	*Notemigonus crysoleucas* (Mitchill)

Carp	*Cyprinus carpio* L.
Yellow perch	*Perca fluviatilis flavescens* (Mitchill)
Bluegill	*Lepomis macrochirus* Raf.
Rockbass	*Ambloplites rupestris* (Raf.)
White crappie	*Pomoxis annularis* Raf.
Brook stickleback	*Culaea inconstans* (Kirtland)
Largemouth bass	*Micropterus salmoides* (Lacépède)
Northern carpsucker	*Carpiodes c. carpio* (Raf.)
Johnny darter	*Etheostoma nigrum* (Raf.)
Iowa darter	*Etheostoma exile* (Girard)
Shiner	*Notropis* sp.

Remarks: It is difficult to decide on the geographical limits of *Anodonta grandis* (*s. str.*) even after studying the large quantity of material on hand. One is tempted to disregard subspecies entirely and to identify all populations seen simply as *A. grandis*, with the possible exception of a few peripheral populations. It is no wonder that numerous names have been applied to *Anodonta* populations where interpopulation variation is of the same magnitude as that observed in the Canadian Interior Basin.

If double-looped, nodulous beak sculpturing is used as the most important character in distinguishing true *Anodonta grandis grandis*, as I believe it should be, then samples 2 to 14 and 16, with the exception of sample 6, form a reasonably homogeneous group (see charts 5 and 10). (Even sample 6 broadly overlaps half of the other samples in the *A. grandis grandis* group with regard to variation in beak sculpture.) The beak sculpture score 2·80 separates the *A. grandis* (*s. str.*) group nearly completely from the other groups. In that group all samples (except 2) have mean values of more than 2·80. In the other groups all samples (except 1) have mean values of less than 2·80. High and low values of Ant. to beak/Length are approximately concordant with these high and low score values of beak sculpture (see charts I and 10). Width/Length and Height/Length values (charts 3, 4, and 10) are partly concordant also. In view of this, I think we are justified in considering as *A. grandis* (*s. str.*), only those populations in the area defined by the records cited above, i.e., the western edge of the Albany River system and the huge Nelson River drainage area (the systems of the Winnipeg, Red and Saskatchewan rivers and the Lake Winnipegosis and Lake Winnipeg drainages), with the exception of some northern populations. A few populations occurring in the southern part of the Churchill River system also appear to be closer to *A. grandis* (*s. str.*) than to *A. g. simpsoniana*.

The records listed include all populations identified as *Anodonta grandis* (*s. str.*). These have also been plotted on Map 8. Several of the samples from the edges of the range were intermediate between *A. grandis* (*s. str.*) and *A. grandis simpsoniana* but are considered to be closer to the former and are therefore classified as *A. grandis* (*s. str.*)

Anodonta grandis grandis appears to have immigrated into the Canadian Interior Basin solely by way of the Red River system during post-Wisconsin confluence of the Red River and the Minnesota River in the region of Lake Traverse and Big Stone Lake. Faunal interchange may have occurred occasionally even up to the early 20th century before the present dam was constructed to stop flood water from overflowing from Lake Traverse (Red River system) into Big Stone Lake (Mississippi River system) across the

low natural divide which separates these drainages.

The present distribution of *Anodonta grandis* in the Hudson Bay drainage area implies that a residual population of *Anodonta* (i.e., *A. g. simpsoniana*) may have already been established over most of the region before *A. grandis* entered the area. See the discussion under *A. g. simpsoniana.*

Anodonta grandis simpsoniana Lea

Simpson's Anodonta;
Plate 5, Figs. 5–10; Map 9.

Anodonta simpsoniana Lea, 1861: *Proc. Acad. natr. Sci. Philad., 5*: 56; 1862: *J. Acad. natr. Sci. Philad., 5*: 212, pl. 32: 281. Type locality: "Fort Rae, Great Slave Lake, Arctic America."

Anodonta kennicottii Lea, 1861 (in part): *Proc. Acad. natr. Sci. Philad., 5*: 56; 1862: *J. Acad. natr. Sci. Philad., 5*: 214, pl. 33: 283. Type locality: "Great Slave Lake at Fort Rae and north end of Lake Winnipeg, Arctic America."

"*Anodonta marginata* Say" of authors but not of Say, 1817. The original description of Say's "species" was published in *Nicholson's Encyclopedia*, 1st Amer. ed., *2*: 19. The type locality was not specified but it is presumably near Philadelphia.

Diagnosis: Shell medium-sized (up to about 5 inches long), ovate or elongate-elliptical, thin, rather fragile, without hinge teeth, periostracum brownish or greenish, and with single-looped or faintly double-looped beak sculpturing which is not nodulous.

Description: *Anodonta grandis simpsoniana* is much like *A. grandis* (*s. str.*) except that the beak sculpturing of *A. g. simpsoniana* consists of 4 to 6 single-looped or faintly double-looped bars which are *not* nodulous (text Fig. 4). In *A. g. grandis* these bars, which also number from 4 to 6, are double-looped and in most specimens are also nodulous. Other differences are statistical and apply to populations and not to individual specimens (see charts 1, 3, 4, and 10; samples 15, 17–30, and A-C below). In general, the umbones tend to be placed farther forward in *A. g. simpsoniana* than in *A. g. grandis* (i.e., Ant. to beak/Length values are lower), Height/Length values are slightly lower, and Width/Length values are also slightly lower and show less inter-population variability than in *A. g. grandis.*

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
(A) Mackenzie River, 2 mi E of Inuvik, N.W.T.					
Length, mm	8	60·2 —83·5	71·3	—	—
Ant. to beak/Length	8	0·220— 0·291	0·246	0·009	0·023
Pt. to base/Height	8	0·359— 0·493	0·445	0·011	0·029
Height/Length	8	0·572— 0·615	0·592	0·006	0·017
Width/Length	8	0·294— 0·335	0·321	0·006	0·014
Beak sculp.	8	1·0—2·0	1·50	0·16	0·42
Periost. colour (percentage Green)	8	62	—	—	—
Periost. colour (Dk.)	8	1·5—1·8	1·75	0·05	0·12
Rays	8	1·0—1·5	1·06	0·10	0·25
Nacre colour	8	3·0	3·0	—	—

Feature	N	Range	Mean	S.E.$_M$	S.D.
(B) Limestone Lake (56°35′N, 96°W) northeastern Man.					
Length, mm	20	30·0 —60·6	46·4	—	—
Ant. to beak/Length	20	0·286— 0·354	0·317	0·004	0·020
Pt. to base/Height	20	0·386— 0·497	0·445	0·007	0·031
Height/Length	20	0·555— 0·658	0·611	0·007	0·030
Width/Length	20	0·293— 0·442	0·358	0·009	0·040
Beak sculp.	20	1·2—3·0	1·86	0·12	0·54
Periost. colour (percentage Green)	20	0	—	—	—
Periost. colour (Dk.)	20	1·0—2·0	1·60	0·06	0·25
Rays	16	1·0—2·0	1·22	0·08	0·31
Nacre colour	20	1·0—2·0	1·35	0·11	0·48
(C) Eastmain River, 16 mi E of Eastmain, Que.					
Length, mm	11	37·3 —71·2	56·0	—	—
Ant. to beak/Length	11	0·200— 0·244	0·225	0·004	0·013
Pt. to base/Height	11	0·377— 0·520	0·422	0·012	0·040
Height/Length	11	0·534— 0·597	0·575	0·006	0·021
Width/Length	11	0·284— 0·368	0·323	0·007	0·025
Beak sculp.	12	1·0—2·0	1·36	0·11	0·37
Periost. colour (percentage Green)	12	0	0	—	—
Periost. colour (Dk.)	12	1·5—2·0	1·63	0·08	0·29
Rays	12	1·0	1·0	—	—
Nacre colour	12	2·0—2·5	2·12	0·07	0·23

The above measurements are those of the 3 northern peripheral samples, A, B, and C, respectively shown on Chart 10. For additional measurements see charts 1–10, samples 15 and 17–30.

Records:

As in *Anodonta grandis grandis*, only specimens examined are listed below.

Southeastern James Bay drainage area. Eastmain River system: Eastmain River, 16 mi E of Eastmain, Que. (this survey). Rupert River system: Lac Waconichi, southern end, 15 mi NE of Chibougamau, Que. (this survey).

Nottaway, Harricanaw, Moose, and Albany River systems. Abundant everywhere.

Attawapiskat River system. Lake Attawapiskat, Ont. (1968, J. V. Wright!). Crow River, Central Patricia, Ont. (this survey).

Ekwan River system. Ekwan River, Ont. (1901, D. B. Dowling!).

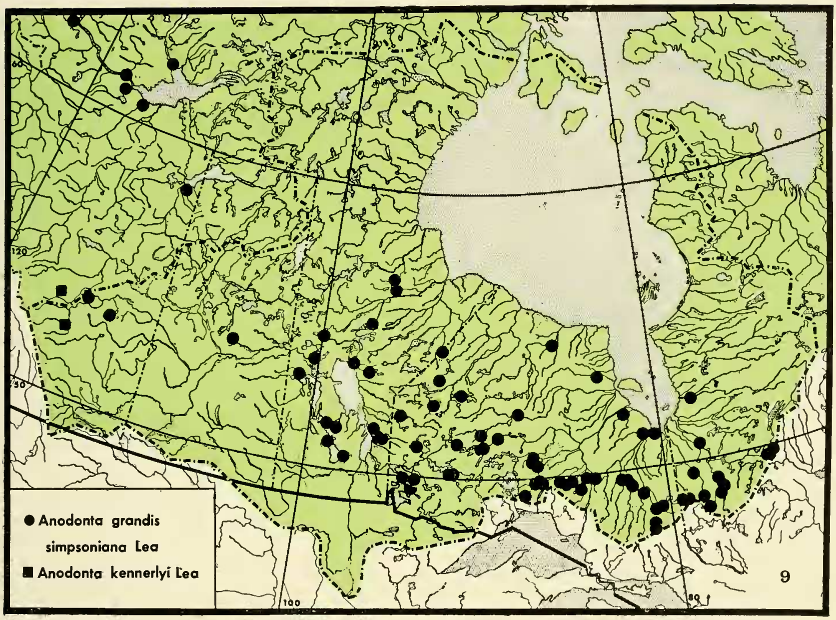
Winisk River system. Winisk River at 54°40′N, 86°15′W, Ont. (1903, W. McInnes!). West Branch Winisk River, Ont. (1905, W. McInnes!).

Severn River system. Unnamed lake at 53°37′N, 92°40′W (headwaters of Sachigo River), Ont. North Spirit Lake, at outlet, Ont. (52°31′N, 93°02′W) (both this survey). Fawn River. Ont. (54°28′N, 88° 16′W) (1967, B. C. McDonald!). Magiss Lake, Ont. (52°59′N, 91°40′W) (Ont. Dept. Lands and Forests!).

Hayes River system. Stull Lake, at outlet, Ont. (54°29′N, 92°37′W) (this survey).

Winnipeg River system. Pelican Lake, Sioux Lookout, Ont. Chukuni River, 2 mi E of Red Lake, Ont. Chadwick's Lake, 15 mi E of Kenora, Ont. (all this survey). Rainy Lake (1886, A. C. Lawson!).

North Saskatchewan River system. Seba Beach, Lake Wabamun, Alta. (1926, L. S. Russell!).



Miquelon Lake, near Camrose, Alta. (1918, R. M. Anderson!). Atkiameg Lake, Man. and Cormorant Lake, Man. (both 1906, W. McInnes!). Candle Lake, Sask. (1962, D. L. Delorme!).

Lake Manitoba-Lake Winnipegosis drainage area. Lake Manitoba at Narrows (1897, J. B. Tyrrell!), at Oak Point (1912, E. M. Kindle!), and at northern end of lake (1888, J. F. Whiteaves!). Fairford River, 6 mi below Fairford, Man. (1888, J. F. Whiteaves!). Lake Winnipegosis, Man., at northeastern corner, 13 mi N of mouth of Red Deer River (this survey).

Nelson River system. Sand River, 33 mi N of Pine Falls Man. Small lake, Manigotogan, 40 mi N of Pine Falls, Man. (both this survey). File River (55°18′N, 100°25′W), Man. (1906, W. McInnes!). Outlet of Lake Winnipeg (1878, R. Bell!). Gunisao River (53°55′N, 97°58′W), Man. (1895, J. B. Tyrrell!). Nelson River (55°15′N, 97°W), Man. (1906, O. O'Sullivan!). Limestone Lake (56°35′N, 96°W), Man. (this survey).

Churchill River system. Lynn Lake, Lynn Lake, Man. Eden Lake (at outlet) (56°38′N, 100° 15′W), Man. Opachuanau Lake (SW arm of Southern Indian Lake), (56°44′N, 99°37′W), Man. (all this survey). Barrington River (56°44′N, 99°44′W), Man. (1966, J. V. Wright!). Recluse Lake (56°55′N, 95°45′W), Man. (this survey).

Mackenzie River system. Athabaska River near Lake Athabaska, Alta, (1943, D. S. Rawson!). Kakisa Lake, N.W.T. (date?, Fish, Res. Bd!). Frank Channel, 3 mi S of Rae, N.W.T. (1944, J. G. Oughton!). Mouth of Hay River at Great Slave Lake, N.W.T. (1919, E. J. Whittaker!). Mills Lake (61°25′N, 118°10′W) and Rocky Lake near Wrigley (63°16′N, 123°37′W), N.W.T. (both 1917, E. M. Kindle!). Mackenzie River 2 mi E of Inuvik, N.W.T. (1966, V. D. Hawley!). Mackenzie River Delta, in lakes at 69°30′N (verbal communication from V. D. Hawley, 1966).

Distribution: This subspecies is known at present only from the Hudson Bay drainage area in Quebec, Ontario, northern Manitoba, northern Saskatchewan, and northern Alberta, and

from the Arctic drainage area of northern Alberta and the Northwest Territories in the Mackenzie River system as far north as the Mackenzie River Delta.

Biology and Ecology: *Anodonta grandis simpsoniana* occurred in ponds and lakes varying from 5 acres in area to the largest lake sampled (Lake Winnipeg). It also occurred in streams ranging from 30 feet to over a mile in width. Substrates occupied were of all types and vegetation was sparse or moderately dense at most stations, as in *A. g. grandis*. See charts 1–10 and the discussion under Genus *Anodonta* for some correlations of ecological factors and morphology. *Lampsilis radiata siliquoidea* was the most frequently associated unionid species. It was found in 40 of the 70 sites from which *A. g. simpsoniana* was taken during this survey.

The anatomy and reproduction of *Anodonta grandis simpsoniana* do not appear to differ from those of *A. g. grandis*. Gravid specimens with glochidia were collected on August 1, 1960 (Wilson Lake, 1½ mi S of Nellie Lake, Ont.) and August 24, 1960 (Lac Dubuisson, 5 mi NW of Val d'Or, Que.). Specimens collected on July 22, 1966 at Limestone Lake, northeastern Manitoba, were placed in an aquarium and shed glochidia between July 24 and 27. No other gravid specimens were found. The glochidia were triangular-ovate and measured from 0·34 mm high and 0·34 mm long to 0·36 × 0·38 mm. As in *A. g. grandis*, " marsupia " containing mature glochidia were thick, pad-like, easily ruptured, and occupied the whole of the outer gills. Fish hosts of *A. g. simpsoniana* are not known but probably many of the same species that are used by *A. g. grandis* are also hosts for *A. g. simpsoniana*.

Remarks on Taxonomy: Although the name *Anodonta simpsoniana* Lea has not been used in the literature since Simpson (1900: 647) synonymized it under *A. kennicotti* Lea, it is the only name which is clearly applicable to the present subspecies. Lea described the beaks of his only specimen of *A. simpsoniana* as much eroded but exhibiting " four rather coarse undulations ". The type specimens of *A. kennicotti* were described as " not perfect in the beaks, but they were enough so to show that they had a double row of granules." I have examined the holotype of *A. simpsoniana* at the United States National Museum (Cat. No. 86434) and it has single-looped beak sculpture similar to that of other specimens in the National Museum of Natural Sciences from Great Slave Lake and elsewhere throughout the range of the subspecies now being considered. The " cotype " of *A. kennicotti* (U.S.N.M. 25712) exhibits tuberculous beak sculpturing and is probably from Lake Winnipeg (not " Great Slave Lake " as stated), an area of intergradation between *A. grandis grandis* and *A. g. simpsoniana*. Since single-looped beak sculpture is the only reliable distinguishing character for this subspecies it would be wrong to use a name founded upon specimens with tuberculous beak sculpturing from an uncertain type locality even though that name (*A. kennicotti*) is better known.

The applicability of several names to this and other subspecies (e.g., *Anodonta benedictensis* Lea, 1834; *A. pepiniana* Lea, 1838; *A. maryattiana* Lea, 1840; *A. footiana* Lea, 1840, etc.) should remain undeclared at least until anatomical examinations and statistical morphological analysis of large collections from most of North America have been made.

Remarks: Although passive transport appears to be particularly probable in *Anodonta*, past stream confluences and drainage history have doubtless been major determinants of present distribution patterns. Fossil anodontas from the late Pleistocene are rare, especially those with discernible beak sculpture still visible, and which can be assigned to subspecies. As far as I am aware, the only such collection available is a lot of 19 complete and fragmentary specimens collected by P. F. Karrow and me from 1 mile E of Alliston, Ontario. The deposits were identified by Dr. Karrow as part of the lower part of upper, post-Pleistocene (Lake Algonquin) sediments. The lot contains 2 specimens with clearly visible beak sculpture consisting of about 4 single-looped bars similar to those seen in many samples of *A. g. simpsoniana*. Lake Algonquin was a precursor of Lake Huron but extended farther east. It occupied an area which is now populated by *Andonta grandis grandis*.

This is not surprising since one would expect that the first immigrants to a newly deglaciated area would be cold-tolerant, and by its present distribution in Canada *Anodonta grandis simpsoniana* is obviously cold-tolerant to a remarkable degree. But the fossils do substantiate to some extent the assumption based on zoogeography that *A. g. simpsoniana* was the earlier invader and that *A. g. grandis* came later and displaced or combined with the resident *A. g. simpsoniana* in western Canada east of the Rocky Mountains.

As mentioned previously, it is difficult to assign some populations from the region of contact between *Anodonta grandis grandis* and *A. g. simpsoniana* to either subspecies with certainty. It is apparent from the material available that gene flow occurs freely between the 2 groups and that they are in fact only subspecifically distinct.

One lot from Quebec is of special interest in this connection, viz., sample 30 from Caché Lake, 5 mi SW of Chibougamau (see charts 1–10). Several of the specimens from that lot are relatively elongate and exhibit 7 to 9 concentric, single-looped beak sculpture ridges which extend much farther out on to the disc than in any other anodontas (except for *Anodonta kennerlyi* from Alberta) seen from the Canadian Interior Basin. In some other specimens the bars are more irregular but still extend far out on the shell. Still other specimens are more ovate and exhibit fewer bars which are slightly double-looped (see chart 5, sample 30). A similar condition exists in sample 29 from Lake Gilman, Chibougamau, Quebec, but the specimens are more uniformly ovate and the beak sculpturing does not extend as far out on to the disc.

The specimens from the Chibougamau district, Quebec, have beak sculpture that closely resembles that of *Anodonta cataracta fragilis* Lamarck from Newfoundland (see Clarke & Rick, 1963). Present information is inadequate to determine if the Quebec populations are actually *A. c. fragilis* or if the similarity is caused by gene flow occurring there between *A. c. fragilis* and *A. g. simpsoniana* now, or at some time in the past. The whole question of whether or not *Anodonta grandis* (*s. lat.*) and *Anodonta cataracta* (*s. lat.*) are reproductively isolated needs reexamination (see Clarke & Berg, 1959). Of at least equal interest would be an investigation of the relationships between *A. c. fragilis*, *A. cygnea* L. of Eurasia and the *A. kennerlyi* group of Western North America. Relationships between the last 2 taxa have been partly but insufficiently considered

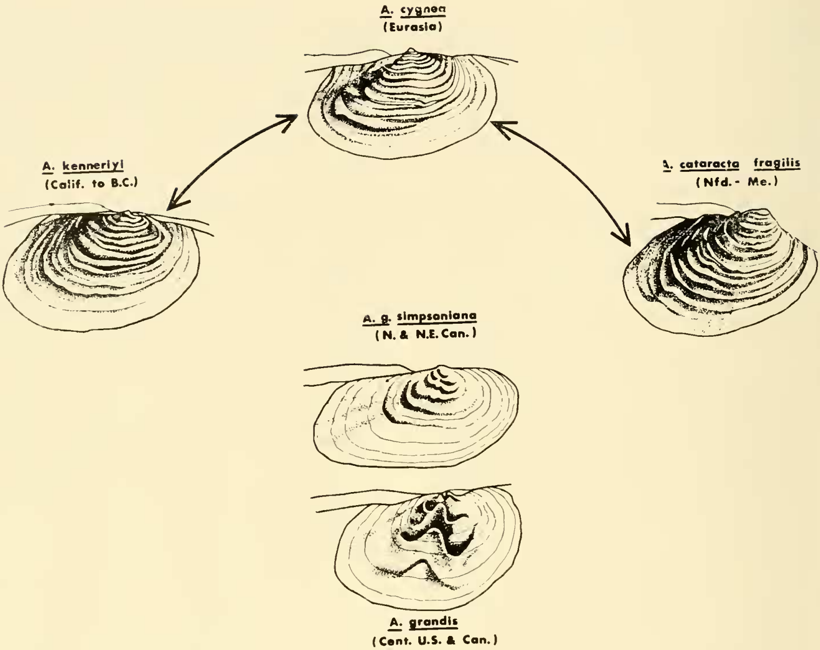


FIG. 4. Beak Sculpturing in *Anodonta*.

by Hannibal (1912: 125). On the basis of beak sculpturing all 3 appear related (see text Fig. 4) and their joint distribution is much like that of the well-known *Margaritifera margaritifera* (L.) group (Clarke, 1967: 26). The *M. margaritifera* group (see Taylor & Uyeno, 1966) is pan-boreal except for its absence in central North America where it may have been extirpated by Pleistocene glaciation. Even *A. g. simpsoniana* has predominantly single-looped beak sculpture suggestive of relationships with the *A. kennerlyi*—*A. cygnea*—*A. cataracta fragilis* group. This relationship appears to be less intimate than that which the 3 latter species have with each other, however.

Anodonta kennerlyi Lea

Western Floater Mussel;
Plate 6, Figs. 1–4; Map 9.

Anodonta kennerlyi Lea, 1860: *Proc. Acad. natr. Sci. Philad.*, *4*: 306; 1862: *J. Acad. natr. Sci. Philad.*, *5*: 108, pl. 18: 256. Type locality: "Chiloweyuck Depot, near Puget Sound, Washington Territory."

Diagnostic Characters: Shell medium-sized, elongate-ovate, thin, and not alate. Beak sculpturing of about eight concentric, irregular bars, which are not nodulous.

Description: (of Alberta specimens). Shell medium-sized (up to about 4 inches long), compressed, elongate-ovate, not alate posteriodorsally, thin (usually cracking on drying), and unsculptured,

except for lines of growth and beak sculpture. Posterior slope dorsally compressed. Periostracum yellowish-brown, greenish-brown, or brown, and many specimens exhibit dark concentric bands or narrow, obscure rays or both. Beaks low, pointed, and projecting slightly above hinge line. Beak sculpture distinct, heavy, variable, and composed of 7 to 10 irregular, concentric bars, which are single-looped to moderately double-looped, but are not at all nodulous (see text Fig. 4). The bars extend farther out on the disc than in *Anodonta grandis grandis* or *A. g. simpsoniana*. Hinge line slightly curved and hinge teeth absent. Nacre white or bluish-white.

Measurements :

Feature	N	Range	Mean	$S.E._M$	S.D.
Crimson Lake, 9 mi N of Rocky Mountain House, Alta.					
Length, mm	38	45·0 —87·3	79·0	—	—
Ant. to beak/Length	38	0·257— 0·358	0·310	0·003	0·020
Pt. to base/Height	38	0·375— 0·585	0·437	0·007	0·041
Height/Length	38	0·487— 0·560	0·527	0·003	0·020
Width/Length	38	0·243— 0·312	0·278	0·003	0·018
Beak sculp.	38	1·0 — 2·5	1·78	0·07	0·43
Periost. colour (percentage Green)	38	24	—	—	—
Periost. colour (Dk.)	38	1·0 — 2·0	1·57	0·04	0·27
Rays	38	1·5 — 3·0	2·11	0·07	0·44
Nacre colour	38	1·0 — 2·0	1·47	0·08	0·50

For comparative measurements of this and other anodontas compare Sample 1 with other samples on charts 1–10 under Genus *Anodonta*.

Records:

North Saskatchewan River system. Crimson Lake 9 mi N of Rocky Mountain House, Alta. (38 valves) (1963, J. C. Cook!).

Athabasca River system. Octopus Lake near Bickerdike, Alta. (2 damaged valves) (collector ?).

Distribution: Oregon to British Columbia (Dall, 1905: 128; Henderson 1929; Ingram, 1948: 78) and Alberta (Clarke, 1967). The National Museum of Natural Sciences has several lots of this species from localities in British Columbia.

Biology and Ecology: No detailed ecological notes on the Alberta specimens are available. Crimson Lake is about 1 square mile in area and has a sand bottom in the region where the shells, which were empty, were picked up. No other unionids were found.

The anatomy of *Anodonta kennerlyi* is described briefly by Lea (1862: 109). Nothing has been recorded concerning its breeding periods, glochidia, or host fish.

Remarks: During the course of examining the anodontas collected from the Canadian Interior Basin, I was much impressed by the prominent differences in beak sculpture between the Crimson Lake material and nearly all other anodontas seen. The beak sculpture was like that which is so typical of the various West Coast " species ", i.e., numerous, irregular bars extending far

out on to the disc (see text Fig. 4). As mentioned under *Anodonta grandis simpsoniana*, the only similar material seen from the Canadian Interior Basin is from Caché Lake and vicinity, near Chibougamau, Quebec, and that is much like *A. cataracta fragilis* from Newfoundland and the Maritime Provinces.

Isaac Lea (1862: loc. cit.), in his remarks under *Anodonta kennerlyi*, wrote: " It reminds one of *fragilis*, Lam., in the colour of the epidermis, and the marks of growth, as well as the thinness of the valves, but it is more transverse, and is rather a smaller species." Lea was probably not aware of the great similarity of the beak sculpturing of the 2 species. That character appears to be an even more significant indication of relationship.

The specimens from Crimson Lake are here referred to as *Anodonta kennerlyi*, principally because that is the least alate of the medium-sized anodontas of the Pacific Coast Region (Ingram, 1948) and the holotype (U.S.N.M. 86533) is much like the Alberta specimens. Further studies may show that *A. kennerlyi* is merely a " conservative " subspecies or infra-subspecies of a normally alate species, i.e., of *A. nutalliana* Lea or *A. oregonensis* Lea, or even of *A. wahlamatensis* Lea. *A. beringiana* Middendorff [=*A. youconensis* Lea] appears to be a much larger and more northern species.

Genus *Anodontoides* Baker

Anodontoides " Simpson " Baker, 1898: *Bull. Chicago Acad. Sci.*, *3*(1): 72. (New name of *Anodontopsis* Baker, 1898 non M'Coy, 1851). Type species: *Anodonta ferussaciana* Lea, by subsequent designation, Simpson, 1900: 658.

Shells small to medium, thin, ovate, sub-inflated, and with a smooth, bright periostracum which may be faintly rayed. Beak sculpture delicate, concentric, and oblique, with radiating ridges posteriorly. Hinge teeth absent; hinge line slightly incurved in front of the umbones. In most specimens the outer gills only are occupied by marsupia. Bradytictic.

Anodontoides contains only a few species and the status of most of them is questionable. The genus occurs in the drainage area of the Gulf of Mexico, Mississippi River, and St. Lawrence River systems and only 1 species, *A. ferussacianus*, lives in the Canadian Interior Basin. Geologic range: Pleistocene to Recent.

Anodontoides ferussacianus (Lea)

Ferussac's Anodonta;
Plate 6, Figs. 5, 6; Map 10.

Anodonta ferussaciana Lea, 1834: *Trans. Amer. phil. Soc.*, *5*: 45, pl. 6: 15. Type locality: " Ohio River, Cincinnati, Ohio."

Anodonta buchanensis Lea, 1838: *Trans. Amer. phil. Soc.*, *6*: 47, pl. 14: 43. Type locality: " Buck Creek, Ohio."

Anodonta subcylindracea Lea, 1838: *Trans. Amer. phil. Soc.*, *6*: 106, pl. 24: 117. Type locality: " Oak Orchard Creek, Orleans County, New York."

Diagnosis : Shell medium-sized, ovate, thin and rather fragile, without hinge teeth, and with *subconcentric*, *oblique* beak sculpture.

Description : Shell small to medium (up to about 3 inches long), subelliptical, inflated, in many specimens entirely without hinge teeth, and with characteristic beak sculpturing. Periostracum greenish or brownish and frequently rayed, especially in young specimens. Posterior outline rounded or biangulate. Beak sculpturing rather fine and composed of several distinctively curved, oblique ridges that are not parallel to the lines of growth (see Pl. 15, Fig. 8). Except for lines of growth and umbonal ridges, the shell is not sculptured. Hinge teeth absent, except

for a slight swelling of the hinge line just in front of the beak. Nacre bluish-white, slightly iridescent, and in many specimens with tints of cream in the beak cavity.

The importance of beak sculpture in the recognition of this species cannot be overemphasized. In *Anodontoides ferussacianus* the beak sculpture is oblique and single-looped and none of the bars is parallel to the lines of growth. In *Strophitus undulatus* the beak sculpture is also single-looped but heavier and the larger, lower bars are approximately parallel to the lines of growth. In *Anodonta grandis* (*s. lat.*) it is single-looped or double-looped and pustulous in many populations. In the single-looped populations the bars are approximately parallel with the lines of growth. Compare Pl. 15, Fig. 8 with text Fig. 4.

Measurements :

Feature	N	Range	Mean	$S.E._M$	S.D.
Pagwachuan River, 75 mi W of Hearst, Ont.					
L, mm	24	44·4 —65·5	53·2	—	—
H/L	24	0·484— 0·554	0·523	0·004	0·018
W/L	24	0·306— 0·377	0·347	0·003	0·017

The only other complete specimens taken during this survey were (1) a single specimen from Souris River, 1/2 mi S of Souris, Man. (L, 77·5; H/L, 0·511; W/L, 0·435); (2) a single specimen from Buffalo River, 3 mi E of Stockwood, Minn. (L, 57·4; H/L, 0·517; W/L, 0·321); and (3) a single specimen (L, 35·4; H/L, 0·573; W/L, 0·328) from Assiniboine River, 3 mi NE of Amsterdam, Sask.

Records:

Albany River system. Pagwachuan River, 75 mi W of Hearst, Ont.; Klotz Lake, 30 mi E of Longlac, Ont. (both this survey).

Winnipeg River system. Kashabowie Lake, Rainy River District, Ont. (Baker, 1939b: 89). Bear River, Minn. and Sturgeon River, Minn. (both, Dawley, 1947: 679). Lake of the Woods (Mozley, 1938: 124). Lake of the Woods, McPherson Island, near Sabaskong Bay (Baker, 1939b: 89).

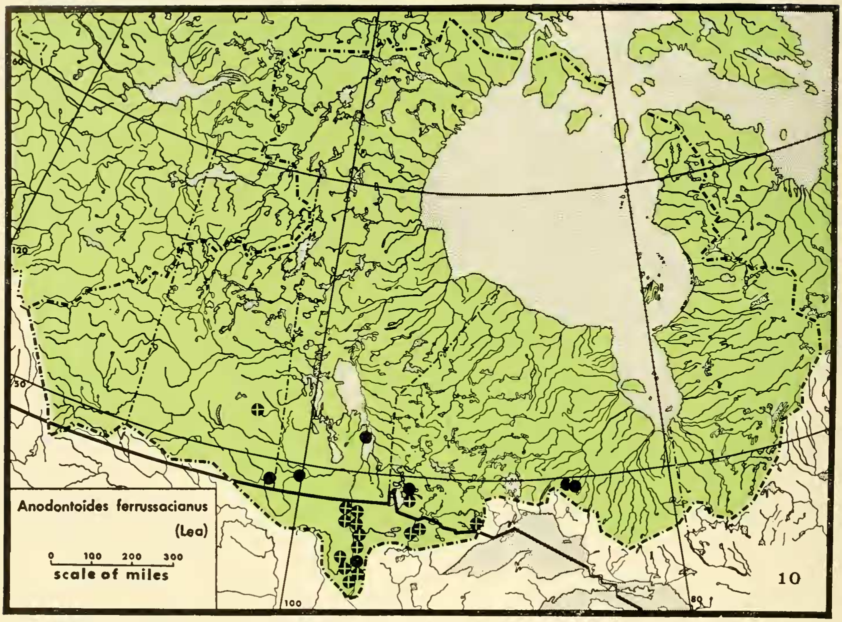
Red River system. Buffalo River, 3 mi E of Stockwood, Minn. Souris River, 1/2 mi S of Souris, Man. Assiniboine River, 3 mi NE of Amsterdam, Sask. Antler Creek, 4 mi W of Carievale, Sask. (all this survey). Also Otter Tail, Wild Rice, Sand Hill, Red Lake, Snake, Middle, Tamarac and Two Rivers rivers, Minn. and Sheyenne, Maple, Turtle, Forest, Park, and Tongue rivers, N.D. (Cvancara, 1967: 189). Outlet of Otter Tail Lake, Minn. (Wilson & Danglade, 1914: 12).

Lake Winnipegosis drainage area. Whitesand River near Theodore, Sask. (Mozley, 1938: 124).

Nelson River drainage area. Lake Winnipeg Mozley, 1938: 124).

Distribution : Ohio-Mississippi River system from Minnesota and Pennsylvania to Colorado and Tennessee. St. Lawrence River system in all the Great Lakes and in many tributaries; also Ottawa River and St. Lawrence River. In the Canadian Interior Basin it occurs in the Albany River system and in many parts of the huge basin ultimately drained by the Nelson River.

Biology and Ecology: In the area under discussion, *Anodontoides ferussacianus* was found to be abundant at only 1 locality, the Pagwachuan River, 75 mi



W of Hearst, Ontario. The river there is approximately 100 feet wide, vegetation was sparse, the current was slow, and the substrate was sand and sandy mud. Single specimens were found in 3 other medium-sized rivers in which the vegetation was sparse or of medium abundance, the current was moderate or slow, and the bottom was mainly of sand or mud or both. A single valve was also found in a large lake (Klotz Lake) with thick vegetation and a sand and mud substrate. In the stream habitats the unionid fauna at 3 localities was dominated (70% to 97%) by *Lampsilis radiata siliquoidea* and at 1 locality (70%) by *Anodonta grandis grandis*.

Ortmann (1911: 294) has found that the anatomy of this species resembles that of *Anodonta*. In Pennsylvania the breeding season lasts from August until the following May. No gravid specimens were seen among the material collected in July and August, i.e., during this survey. The glochidia are reported to measure about 0·32 mm in height and length, to be sub-triangular, and to bear hooks. The northern muddler, *Cottus bairdii* Girard, is a host fish for this species (J.P.E. Morrison, pers. comm.).

Remarks: *Anodontoides ferussacianus* is much like other unionids in that it is morphologically variable and that these variations do not correlate with geography and are presumed to be ecophenotypic. Like other variable species it has received several varietal names which are currently, and incorrectly, used subspecifically. Both *A. f. buchanensis* and *A. f. subcylindracea* are reported as small stream ecophenotypes of *A. f. ferussacianus*, differing from

the nominate subspecies in increased relative obesity. Both these obese and the normal phenotypes sometimes occur together, however, and are then connected by intergrades. In the Pagwachuan River material, the range in variation in H/L and W/L ratios broadly overlap the dimensions given for *ferussacianus* (*s. str.*), *buchanensis*, and *subcylindracea* by Baker (1928b: 176–9) and by Ortmann (1919: 166–170). Clearly, *buchanensis* and *subcylindracea* are not valid subspecies of *A. ferussacianus.*

The status of *Anodontoides modestus* (Lea) and *Anodontoides birgi* Baker is also questionable. These taxa are differentiated from *Anodontoides ferussacianus* chiefly on beak sculpture characters and until a more thorough investigation is carried out to determine the natural variability of beak sculpture in *Anodontoides* their status cannot be evaluated.

Genus *Strophitus* Rafinesque

Strophitus Rafinesque, 1820: *Ann. Gén. Sci. Phys.*, Brussels, *5* (13): 316 (Binney & Tryon reprint, 1864: 59). Type species: *Anodonta undulata* Say, by monotypy.

Shells medium-sized, thin to slightly thickened, elliptical to rhomboid, inflated, sub-pointed to biangulate posteriorly, and with a low posterior ridge which is double in some specimens. Umbones sculptured with a few, strong, concentric ridges which curve sharply upward posteriorly. Periostracum with or without rays. Hinge teeth rudimentary. Sexual dimorphism in shell characters absent. Marsupia occupying the whole of the outer gills and consisting of short, horizontal ovisacs which are oriented perpendicular to the surface of the gills. Bradytictic.

Strophitus contains about 8 species and subspecies and is distributed throughout eastern and central North America from the Canadian Interior Basin to the Gulf of Mexico and from the Atlantic Coast west at least to Saskatchewan. Geologic range: Recent.

Strophitus undulatus (Say)

Squawfoot Mussel;
Plate 6, Figs. 7, 8; Map 11.

Anodonta undulata Say, 1817: *Nicholson's Encyclopedia*. 1st. Amer. ed., *2*: 20–21, pl. 3:6 (Binney reprint, 1858: 54). Type locality not specified but probably near Philadelphia.

Anodonta pensylvanica Lamarck, 1819: *Animaux sans Vertébres*. *6*(1): 86. Type locality: "la rivière Schuglkill, près de Philadelphie."

Anodon rugosus Swainson, 1822: *Zool. Illus.*, (1st ser.) *2*, pl. 96. Type locality: "United States."

Alasmodonta edentula Say, 1829: *N. Harmony Dissem. useful Knowl.*, *2*: 340 (Binney reprint, 1858: 137). Type locality: "Wabash River."

Anodonta pavonia Lea, 1836: *Trans. Amer. phil. Soc.*, *6*: 78, pl. 21: 65; 1838: Observations *2*: 78, pl. 21: 65. Type locality: "Head waters of the Little Beaver, Ohio."

Strophitus rugosus pepinensis F. C. Baker, 1928: *Fresh Water Mollusca of Wisconsin*, *2*: 204, pl. 74: 8. Type locality: "Lake Pepin, near Lake City, Minn."

Strophitus rugosus winnebagoensis F. C. Baker, 1928: *Ibid.*, p 205, pl. 74: 1–6. Type locality: "Long Point Island, Lake Winnebago" [Wisconsin].

Strophitus rugosus lacustris F. C. Baker, 1928: *Ibid.*, p 207, pl. 75: 6–8. Type locality: "Oconomowoc Lake, Waukesha Co., Wisconsin."

Diagnosis: Shell medium-sized and rather thin; with dark periostracum; coarse, single-looped, beak sculpturing approximately parallel with the lines of growth; with vestigial pseudocardinal teeth barely evident; and with no trace of lateral teeth.

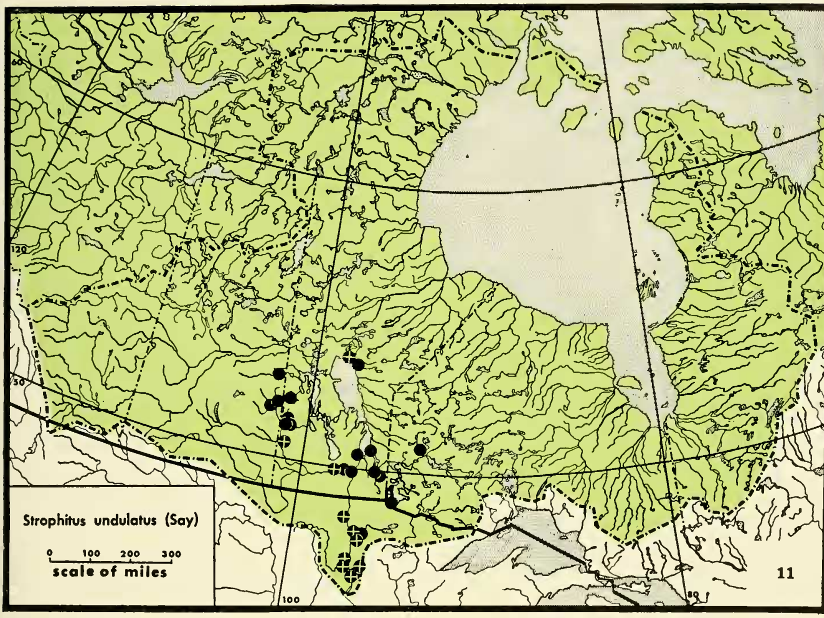
Description: Shell variable, of medium-size (up to about 4 inches long) subelliptical, thin when young to slightly thickened when adult, subinflated, and nearly edentulous. Periostracum yellowish- or greenish-brown to blackish-

brown and, in young specimens, with green rays. Beak sculpture of rather coarse, centrally flattened, single-looped ridges which, in general, are approximately parallel with the lines of growth (Pl. 15, Fig. 9). Pseudocardinal hinge teeth of most specimens indicated by swellings just anterior to the beaks or by low, rounded excrescences in each valve. One sometimes sees specimens with small, clearly discernible, pseudocardinal teeth. Lateral teeth absent. Nacre white in the largest specimens or, more usually, bluish-white with suffusions of yellow or salmon in and near the beak cavities. At the border of each valve a narrow band of olive green or greenish-brown is also present.

Measurements:*

Feature	N	Range	Mean	$S.E._M$	S.D.
Red Lake River, Crookston, Minn.					
L, mm	11	46·0 —74·8	60·4	—	—
H/L	11	0·513— 0·584	0·536	0·007	0·022
W/L	11	0·315— 0·403	0·335	0·007	0·024
Ant. to beak/Length	11	0·275— 0·335	0·302	0·006	0·020
Lake Winnipeg, near mouth of Winnipeg River, Man.					
L, mm	4	54·2 —60·2	58·3	—	—
H/L	4	0·598— 0·648	0·626	—	—
W/L	4	0·374— 0·395	0·386	—	—
Ant. to beak/Length	4	0·276— 0·351	0·315	—	—
Lake Winnipeg, 20 mi S of Gimli, Man.					
L, mm	9	36·6 —48·7	41·2	—	—
H/L	9	0·569— 0·634	0·601	0·012	0·037
W/L	9	0·321— 0·360	0·343	0·007	0·021
Ant. to beak/Length	9	0·246— 0·292	0·273	0·008	0·024
Shell River, 9 mi NNE of Roblin, Man.					
L, mm	15	35·8 —89·5	58·0	—	—
H/L	15	0·507— 0·584	0·564	0·005	0·018
W/L	15	0·282— 0·360	0·319	0·005	0·020
Ant. to beak/Length	15	0·263— 0·319	0·301	0·004	0·014
Red Deer River, 4 mi S of Hudson Bay, Sask.					
L, mm	40	44·8 —82·4	63·0	—	—
H/L	40	0·517— 0·593	0·555	0·002	0·016
W/L	40	0·270— 0·359	0·307	0·003	0·019
Ant. to beak/Length	40	0·241— 0·318	0·283	0·003	0·019

* Ant. to beak/Length is a measure of the relative position of the umbones (see Genus *Anodonta*).



Records:

Winnipeg River system. Chukuni River, 3 mi N of Packwash Lake, Ont. (this survey). Winnipeg River, Ont. (Mozley, 1926: 122). Whitemouth River near Whitemouth, Man. Birch River near McMunn, Man. (both this survey). " Rocky Point ", Lake of the Woods, [Minn.?] (Univ. Minn.!).

Red River system. Red River, Wilkin Co., Minn. and Red Lake River, Crookston (both Univ. Minn.!). Sheyenne River, Argusville, N.D. (Ortmann, 1919: 203). Otter Tail, Sand Hill, and Red Lake rivers, Minn. and Sheyenne, Turtle, Forest, and Pembina rivers, N.D. (all Cvancara, 1967: 189). Otter Tail Lake outlet, Minn. West Lost Lake outlet, Minn. Otter Tail River, Perham, Minn. (all Wilson & Danglade, 1914: 12). Assiniboine River: western edge of Winnipeg, Man.; 12 mi NW of St. Francis Xavier, Man.; and 3 mi NE of Amsterdam, Sask. (all this survey). Birdtail Creek near Birtle, Man. (Mozley, 1938: 123). Shell River: 6 mi E, 8 mi E, and 9 mi NNE of Roblin, Man. (all this survey).

Lake Winnipegosis drainage area. Swan River, 8 mi N of Norquay, Sask. Red Deer River, 4 mi S of Hudson Bay, Sask. Woody River, 8 mi N of Swan River, Man. (all this survey).

Saskatchewan River system. Saskatchewan River (Mozley, 1938: 123).

Nelson River system. Lake Winnipeg: 20 mi S of Gimli, Man. (this survey) and mouth of Winnipeg River (" below Elk Island and Fort Alexander ") (1883, R. Bell!). Gunisao River, Man. (1895, J. B. Tyrrell!). Playgreen Lake (Mozley, 1938: 123).

Mackenzie River system. Mouth of Hay River, 60°51′N (Whittaker, 1924). This record needs confirmation; it is probably incorrect.

Distribution: Ohio-Mississippi River system from Minnesota to Texas and from Pennsylvania to Tennessee. Atlantic drainage area from Nova Scotia to North Carolina. Canadian Interior Basin in the Nelson River drainage area from western Ontario to Saskatchewan.

Biology and Ecology: *Strophitus undulatus* occurred most abundantly in the Red

Deer River 4 mi S of Hudson Bay, Sask. and in Chukuni River 3 mi N of Packwash Lake, Ont. These rivers are approximately 100 and 125 feet wide, respectively, with sparse vegetation, a rapid current, and a bottom composed of mud, sand, and rocks. Other localities are rivers of various widths (25 to 150 feet) and depths (mainly less than 4 feet) with sparse vegetation predominating. Current varied from slow to rapid and all bottom types, clay, mud, sand, gravel, and rocks, were encountered. Stunted, empty specimens were also common on the semi-exposed shore of Lake Winnipeg 20 mi S of Gimli, Man.

Strophitus undulatus was taken at 13 stations during this survey. The most abundant unionids at 12 of these localities were *Lampsilis radiata siliquoidea* and *Anodonta grandis grandis*. The former was dominant at 7 localities and the latter at 5. At 1 locality, Chukuni River, *Strophitus undulatus* was dominant.

The anatomy and reproduction of this species have been discussed by Ortmann (1911: 299), Lefevre & Curtis (1911: 863), and Baker (1928b: 200). The breeding season in Pennsylvania lasts from July to the following April or May. None of the specimens collected in the Canadian Interior Basin (all taken from mid-July to mid-August) were gravid. In 1 lot of 3 specimens collected in the Chateauguay River, 5 mi W of Howick, Que. (St. Lawrence River drainage) on August 14, 1960, all were gravid, however. The glochidia were held firmly within the marsupia, were subtriangular and almost bean-like in shape, and measured 0·46 mm long and 0·36 mm high. Ortmann (op. cit.) reported the glochidia as subtriangular, with hooks, and measuring approximately 0 36 mm long and 0·30 mm high. Unlike other unionids, the ovisacs of each water tube are subdivided into a number of compartments, each containing a well-developed placentula placed transversely to the tube. The placentulae persist until their contents are discharged.

Lefevre & Curtis (1911 : 863) reported that in *Strophitus undulatus* metamorphosis from the glochidium to the juvenile stage may take place without a period of attachment on fish. Successful metamorphosis on fish (largemouth black bass, *Micropterus salmoides* (Lacepède) and northern creek chub, *Semotilus atromaculatus* (Mitchill)) has also been reported (Baker, 1928b: 201). Although both these fishes are widely distributed, neither is known to range as far west as does *S. undulatus*, i.e., to Saskatchewan.

Remarks: With the exception of the Chukuni River locality (total hardness 38 ppm) in the Canadian Interior Basin *Strophitus undulatus* has been found only in hard-water regions. Expansion of its range beyond the vicinity of the Red River has been almost entirely toward the north and west and hardly at all toward the east or northeast on to the Precambrian Shield. This contrasts with its behaviour in eastern North America where it occurs in both hard- and soft-water habitats.

Aside from shell size and thickness differences between populations, attributable to differences in food supply, growing season, and water hardness, morphological characters that will distinguish mid-continental populations from eastern populations have not been found. It appears possible that a different physiological subspecies is present in each area. An equally plausible explanation, however, may be that *Strophitus undulatus* in the Canadian Interior Basin is at the climatic limit of its range and, in

such a marginal region, is only able to survive in the more favourable environments afforded by hard water.

Simpson (1900: 616–18) reduced numerous specific names to synonymy under *Strophitus edentulus* Say, *S. edentulus* var. *pavonius* Lea, and *S. undulatus* Say. In my opinion these 3 names are also synonymous. Since then Baker (1928b: 204–7) has described 3 additional " varieties " (*S. rugosus pepinensis*, *S. r. winnebagoensis*, and *S. r. lacustris*) based principally on the relative position of the beaks, a variable character which may be responsive to ecological differences (see Ant. to beak/Length ratios under " Measurements ", also see discussion under Genus *Anodonta*). Although these were given trinomial names they were not intended to represent geographical subspecies and are at best only ecophenotypes.

Subfamily Lampsilinae von Ihering

Lampsilinae von Ihering, 1901: *Nautilus*, *15*: 53. Type genus: *Lampsilis* Rafinesque.

Shells small to large, thin or thickened, sculpturing various, and hinge teeth well developed in most species. Sexual dimorphism in shell characters apparent in all but a few genera. In some genera, e.g., in *Dysnomia*, sexual dimorphism is extreme. Bradytictic, females retaining the glochidia in the marsupia at least from fall to the following spring. Marsupia in most species formed by the posterior part of the outer gill, rarely by the whole gill. Water tubes not divided in the gravid female as in the Anodontinae. Glochidia semicircular or semielliptical and without hooks except in *Proptera* in which they are axe-head shaped and have 2 hooks on each valve.

About 160 species of Lampsilinae are at present considered to be valid. The subfamily is exclusively North American and ranges from Mexico to near the tree-line and from the Atlantic Coast to the Rocky Mountains. Geologic range: Triassic (?) or Lower Oligocene to Recent.

Genus *Proptera* Rafinesque

Proptera Rafinesque, 1819: *J. Phys. Chim. Hist. natr.*, etc., *88*: 426. (Binney & Tryon reprint, 1864: 29). Type species: *Unio alata* Say, by subsequent designation, Herrmannsen, 1847. (In 1820 Rafinesque emended *Proptera* to *Metaptera* and Herrmannsen's type selection was for the latter. Since the 2 are objective synonyms, *Unio alata* is also the type species of *Proptera*).

Shells ordinarily large, of medium thickness, gaping at the anterior edge and at the edge of dorsal slope, and with a high dorsal wing in juveniles and in many adults. Beak sculpture feeble and concentric. Periostracum rayless or obscurely rayed and brown or blackish in colour. Hinge teeth compressed, pseudocardinals commonly incomplete and widely separated from the laterals. Sexual dimorphism of the shell apparent. Marsupia occupying the posterior part of the outer gills. Edge of mantle in females slightly lamellar in front of the branchial opening and with granulations but without papillae. Glochidia axe-head shaped, with 2 spines, 1 at each of the ventral corners. Bradytictic.

Approximately 8 species of *Proptera* are known. They occur in the Gulf of Mexico drainage from Mexico to Alabama, in many parts of the Mississippi-Missouri River and St. Lawrence River systems, and in the Canadian Interior Basin in the Red River system. Geologic range: Pleistocene to Recent.

Proptera alata (Say)

Pink Heel-splitter;
Plate 7, Figs. 1, 2; Map 12.

Unio alatus Say, 1817: *Nicholson's Encyclopedia*, 1st. Amer., ed., *1*, pl. 4: 2 (Binney reprint.

1858: 52). Type locality not specified. Another specimen mentioned by Say, but not the one described, is cited from Lake Erie.

Metaptera megaptera Rafinesque, 1820: *Ann. Gén. Sci. Phys.*, Brussels, *5*(13): 300, pl. 80: 20–22 (Binney & Tryon reprint, 1864: 44). Type locality: "dans l'Ohio."

Diagnosis: Shell medium to large, ovate, relatively compressed, with dark periostracum, purple nacre, well-developed hinge teeth, and a prominent dorsal "wing."

Description: Shell rather large (up to about 5 inches long in our specimens but larger elsewhere), ovate, rather thin, and with a prominent dorsal projection or "wing." Projection triangular and high; in old specimens it may be of medium height or lower. Periostracum greenish-brown to brown in young specimens, brown or blackish in adults, and with or without poorly defined rays. Beak sculpture single-looped or slightly double-looped but not prominent (Pl. 15, Fig. 10). Pseudocardinal teeth conical, serrate, of medium size, 1 or 2 in the right valve and 2 in the left. Lateral teeth elongate, elevated, curved, single in the right valve and double in the left, though fused anteriorly. Nacre purple to pink and iridescent.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Red River, St. John Baptiste, Man.					
L, mm	4	86·0 —100·2	91·6	—	—
H/L	4	0·702— 0·811	0·744	—	—
W/L	4	0·312— 0·358	0·340	—	—
Red Lake River, Crookston, Minn.					
L, mm	15	65·0 —127·4	100·2	—	—
H/L	15	0·688— 0·772	0·732	0·007	0·028
W/L	15	0·317— 0·388	0·346	0·005	0·020

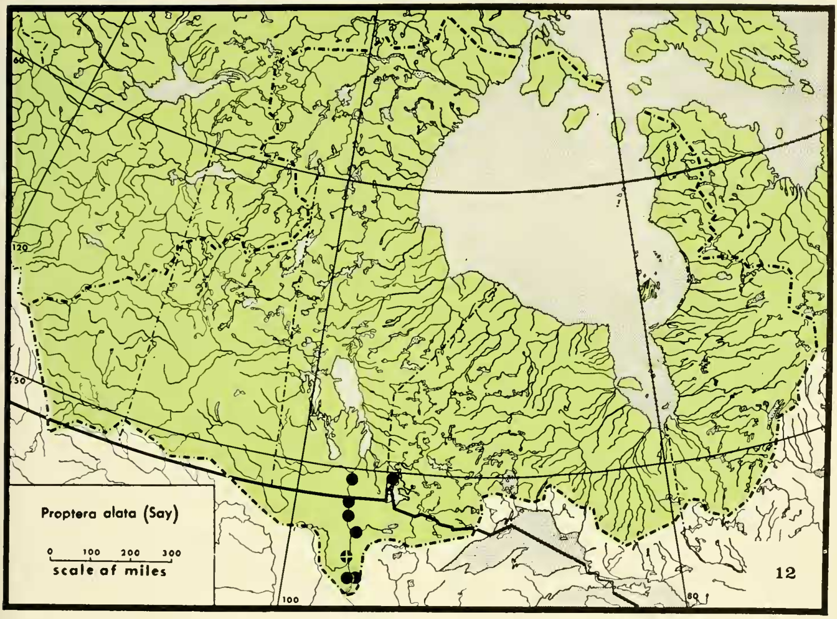
Records:

Winnipeg River system. Near Lake of the Woods, Ont. (Mozley, 1938: 125).

Red River system. Red River: Abercrombie, N.D.; 2 mi NE of Drayton, N.D. (both this survey); Wilkin Co., Minn.; Pembina, N.D. (both Univ. Minn.); St. Norbert, Man. (empty valves, this survey). Sheyenne River, N.D. (empty valves, Cvancara, 1967: 189). Red Lake River, Crookston, Minn. (Univ. Minn. and Cvancara 1967: 189). Sand Hill River, Climax, Minn. (this survey).

Distribution: Ohio-Mississippi River system from Minnesota to Pennsylvania and Kansas to Alabama. St. Lawrence River system from Lake Huron to Lake Champlain in the major lakes and in many tributaries. Canadian Interior Basin in parts of the Winnipeg River and Red River systems.

Biology and Ecology: During this survey *Proptera alata* was found only in rivers exceeding 40 feet in width with sparse vegetation and with moderate current. In 5 of the 6 localities the bottom was mainly mud; in the other it was sand and gravel. At each



locality *P. alata* was a minor element of a diverse mussel fauna containing from 6 to 10 species. As usual, the dominant species at most of these localities was either *Lampsilis radiata siliquoidea* or *Anodonta grandis grandis*.

The anatomy of *Proptera alata* has been discussed by Ortmann (1911: 333). In Pennsylvania it breeds from August to the following July. Only 1 gravid specimen was taken during this survey, on August 3, 1964, from the Red River at Abercrombie, N.D. This contained developing eggs, oblong-ovate in shape, and rather variable in size but measuring approximately $0{\cdot}20 \times 0{\cdot}40$ mm.

The glochidia of *P. alata* are distinctively axe-head shaped, with 2 spines on each valve, and are reported to measure from 0·20—0·23 mm in width and 0·38—0·41 mm in height (Ortmann, loc. cit.) The host fish is unknown.

Remarks: The name *Proptera alata alata* has been used by many authors for the stunted ecophenotype occurring in lakes. *P. alata megaptera* has been widely applied to the larger ecophenotype occurring in rivers. Such populations are not subspecies. In fact, since there is no justification for believing that Say's *Unio alata* actually came from a depauperate lake population the name is not even available as an infrasubspecific name for the lake ecophenotype. *Metaptera megaptera* is simply a synonym of *Unio alata*.

Genus *Ligumia* Swainson

Ligumia Swainson, 1840: *A treatise on malacology*, etc., London, p 267–378 (in error as *Ligumea*, p 263). Type species: *Unio rectus* Lamarck, by monotypy.

Shells ovate to elongate-elliptical, of moderate thickness, and smooth. Umbones delicately sculptured with double-looped ridges. Females expanded post-basally. Hinge teeth well-developed and medium sized. Inner edge of the mantle in the female distinctly papillate. Marsupia occupying the posterior part of the outer gills only. Bradytictic.

Ligumia contains only a few species and is distributed throughout the Atlantic, Gulf of Mexico, Mississippi-Missouri River, and St. Lawrence River drainage areas. One species, *L. recta*, has penetrated into the south-central part of the Canadian Interior Basin. Geologic range: Pleistocene to Recent.

Ligumia recta (Lamarck)

Black Sand Shell;
Plate 8, Figs. 1–4; Map 13.

Unio recta Lamarck, 1819: *Animaux sans Vertèbres*, *6*: 74. Type locality: " lac Erie."
Unio latissima Rafinesque, 1820: *Ann. Gen. Sci. Phys.*, Brussels, *5*(13): 297, pl. 80: 14–15 (Binney & Tryon reprint 1864: 42). Type locality: " la rivière Ohio."

Diagnosis: Shell large, elongate, rather thick, with complete hinge teeth, dark (and often rayed) periostracum, and white or purple nacre.

Description: Shell moderately large (up to about 5 inches long), elongate-elliptical, rather thick and heavy, strong, and slightly inflated. Sexual dimorphism in the shell well-marked; females typically expanded post-basally. Periostracum smooth, greenish or blackish and obscurely rayed in adults but paler and prominently rayed in many juveniles. Rays, when present, are dark green. Beak sculpture typically faint and double-looped (see Pl. 15, Fig. 11). Pseudocardinal teeth elevated, compressed, serrated, double in the left valve and single or double in the right. Lateral teeth erect, elongate, single in the right valve and double in the left. Nacre entirely silvery-white, with purple suffusions near the beak cavity, or entirely purple.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Red River, 2 mi NE of Drayton, N.D. (males).					
L, mm	4	95·7 —119·1	106·5	—	—
H/L	4	0·426— 0·444	0·431	—	—
W/L	4	0·249— 0·275	0·262	—	—
Assiniboine River, western edge of Winnipeg, Man. (males).					
L, mm	12	93·9 —120·7	111·3	—	—
H/L	12	0·432— 0·475	0·450	0·004	0·013
W/L	12	0·241— 0·296	0·265	0·006	0·018

Feature	N	Range	Mean	S.E.$_M$	S.D.
Red River, St. John Baptiste, Man. (females).					
L, mm	4	88·2 —107·5	97·8	—	—
H/L	4	0·432— 0·476	0·458	—	—
W/L	4	0·246— 0·314	0·258	—	—
Assiniboine River, western edge of Winnipeg, Man. (females).					
L, mm	6	102·2 —109·3	106·0	—	—
H/L	6	0·449— 0·502	0·484	0·008	0·020
W/L	6	0·276— 0·314	0·291	0·005	0·013

Records:

Winnipeg River system. Lake of the Woods, Ont. (Mozley, 1938: 125). Whitemouth River near Whitemouth, Man. (1951, W. E. Godfrey!; also this survey).

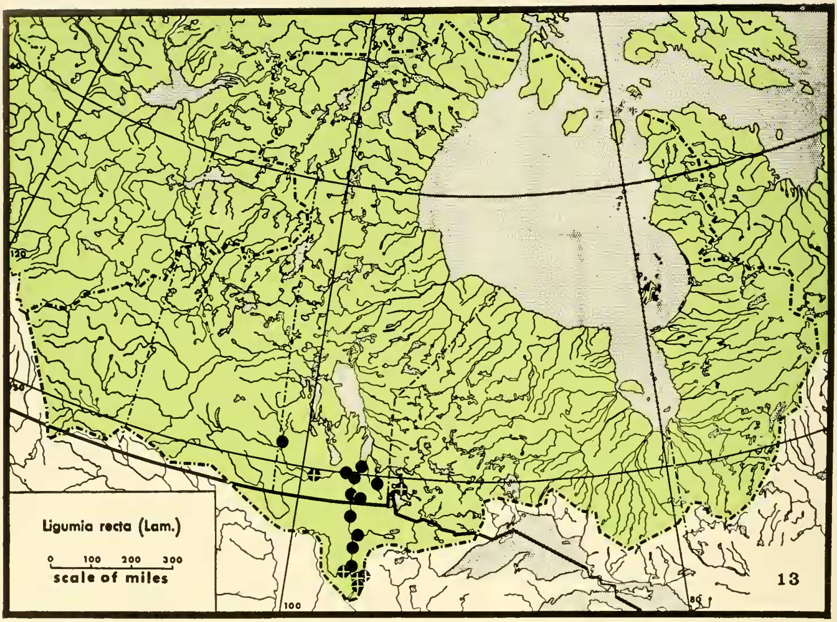
Red River system. Red River: 3 mi W of Nielsville, Minn.; 2 mi NE of Drayton, N. D.; Abercrombie, N.D.; and St. John Baptiste, Man. (all this survey). Otter Tail River, Minn.; Sheyenne River, N.D. (both Cvancara, 1967: 189). Little Pine Lake outlet; Otter Tail Lake outlet; West Lost Lake outlet; and Otter Tail River at Perham and below Fergus Falls, Minn. (all Wilson & Danglade, 1914: 12). Red Lake River, Minn. (Univ. Minn. and Cvancara, 1967: 189). Sand Hill River, Climax Minn.; Roseau River, 8 mi N of Tolstoi, Man.; Assiniboine River: western edge of Winnipeg, Man.; 12 mi NW of St. Francis Xavier, Man. (all this survey); Aweme, Man. (Mozley, 1938: 125); and Millwood, Man. (1888, J.B.Tyrrell!).

Nelson River system. Fort Garry, Lake Winnipeg (1883, R. Bell!).

Distribution: Ohio - Mississippi river system from Minnesota to Pennsylvania and Oklahoma to Alabama. Alabama River system in Georgia and Alabama. St. Lawrence River system from Lake Huron to Lake Champlain, the Ottawa River, and the vicinity of Montreal. Canadian Interior Basin in the Red River and Winnipeg River systems and Lake Winnipeg.

Biology and Ecology: *Ligumia recta* was found only in rivers during this survey and, in all cases but 2, exclusively in rivers exceeding 100 feet in width. (Elsewhere it also occurs in lakes and possibly will be found in lakes in the Candian Interior Basin also.) The exceptions, Sand Hill River, Climax, Minn. and Whitemouth River near Whitemouth, Man., are rivers about 40 and 50 feet wide respectively. In every case aquatic vegetation was sparse to moderate in abundance, current was predominantly moderate, and the bottom was either of mud or of sand or a mixture of both, with or without gravel and rocks. At each of these localities *L. recta* constituted only a minor element of a unionid fauna consisting of 6 to 10 species and dominated in most cases by the ubiquitous *Lampsilis radiata siliquoidea*.

The anatomy of this species has been discussed by Ortmann (1911: 345) by Utterback (1916: 440) and by Baker



(1928b: 258). The inner edge of the mantle bears well-developed papillae in front of the branchial opening. *Ligumia recta* is reported to breed from August to the following July. During this survey gravid females were found containing developing eggs on June 6, 1965, on August 4, 1964, and on August 17, 1961, and with mature glochidia on July 6, 1964. Specimens collected in mid-July contained empty ovisacs. The glochidia observed were purse-shaped, ovate, and measured 0·23 mm in length and 0·27 mm in height.

Host fish for the glochidia of *L. recta* are reported to be the bluegill, *Lepomis macrochirus* Rafinesque and the white crappie, *Pomoxis annularis* Rafinesque.

Remarks: Here is another case in which river populations and lake populations have been incorrectly recognized as distinct subspecies. *Ligumia recta* (*s. str.*) has been broadly applied to the smaller ecophenotype occuring in lakes and *L. recta latissima* to the larger, more compressed ecophenotype occurring in rivers. These are not geographic subspecies and the distinction is only of infrasubspecific value.

Genus *Lampsilis* Rafinesque

Lampsilis Rafinesque, 1820: *Ann. Gén. Sci. Phys.*, Brussels, *5*(3): 298 (Binney & Tryon reprint, 1864: 43). Type species: *Unio ovatus* Say, by subsequent designation, Herrmannsen (1846: 575).

Shells medium-sized to large, elliptical to subcircular in outline, and of moderate thickness and inflation. Umbones prominent and sculptured with double-looped ridges. Periostracum smooth to slightly roughened and commonly with well-

marked rays. Hinge teeth well-developed but not large. Sexual dimorphism of the shell is clearly apparent in most species, the females being expanded post-basally. Marsupia occupying the posterior part of the outer gills only. Edge of the mantle in females modified and forming a ribbon-like flap which is produced anteriorly as an irregular, projecting lobe. Bradytictic.

Lampsilis contains approximately 25 species and is distributed throughout North America east of the Rocky Mountains and north nearly to the tree-line (see *Lampsilis radiata siliquoidea*, below). Two species occur in the Candian Interior Basin. Geologic range: Triassic (?) or Lower Oligocene to Recent.

Lampsilis radiata siliquoidea (Barnes)

Fat Mucket; Plate 10, Figs. 1–5; Map 14.

Unio siliquoideus Barnes, 1823: *Amer. J. Sci.*, *4;* 263, pl. 13: 150. Reprinted in *Sterkiana*, (7): p 13–14 (1962). Type locality: " Inhabits the Wisconan [*sic.*, Wisconsin River]."

Unio superiorensis Marsh, 1897: *Nautilus*, *10:* 103, pl. 1: 1, 2, 5. Type locality: " Michipicoton [*sic.*, Michipicoten] River, upper shore of Lake Superior, Canada."

Not *Unio luteolus* Lamarck, 1819: *Animaux sans Vertebres*. *6:* 79. Type locality: " la rivière Susqueshana et celle Mohancks, dans les États-Unis." See " Remarks."

Diagnosis: Shell medium-sized, elliptical, sexually dimorphic (posteriorly enlarged in females), with numerous prominent, dark coloured rays and well-developed hinge teeth.

Description: Shell medium-sized (up to nearly 5 inches in length), subelliptical, swollen posterio-ventrally in the females, not swollen in the males; shell thicker anteriorly and thinner posteriorly, strong, and subinflated. Periostracum yellowish, greenish, or brownish, and smooth and shiny. Rays greenish or blackish, generally distributed, and mostly narrow and sharply defined. Beak sculpturing consisting of numerous bars each with a shallow central sinuation (Pl. 15, Fig. 12). Pseudocardinal teeth medium in size, erect, directed forward, compressed, and serrated, most frequently with 2 in each valve. Lateral teeth prominent, narrow, straight or slightly curved, 1 in the right valve and 2 in the left. Nacre white or bluish-white and iridescent posteriorly.

Measurements: (see Table 5, p 106)

The following abbreviations, in addition to those used in previous sections (e.g., see Chart 1 caption under Genus *Anodonta*), are used here.

Hb: height taken at umbo and perpendicular to the long axis.

Hp: height taken at the posterior termination of the ligament. The ratio Hp/Hb is approximately equivalent to the ratio B/A used by Clarke & Berg (1959: 68).

Rays: a score derived by comparison with a standard series graded from 0 to 7 in which 0 = rays absent; 1 = rays very narrow; 2, 3, 4, 5, and 6 = rays of progressively greater width; and 7 = very wide rays. The same standard series of specimens was used by Clarke & Berg (1959: 68) in a previous study of variation in *Lampsilis*.

Records:

Approximately 200 lots are available, so only marginal records are cited.

Nottaway River system. O'Sullivan River, 1/2 mi N of Miquelon, Que. Bell River, 33 mi N of Senneterre, Que. (both this survey).

Harricanaw River system. Lac Dubuisson (Lac de Montigny), 5 mi NW of Val d'Or, Que. Lac La Motte, 25 mi NW of Val d'Or (both this survey).

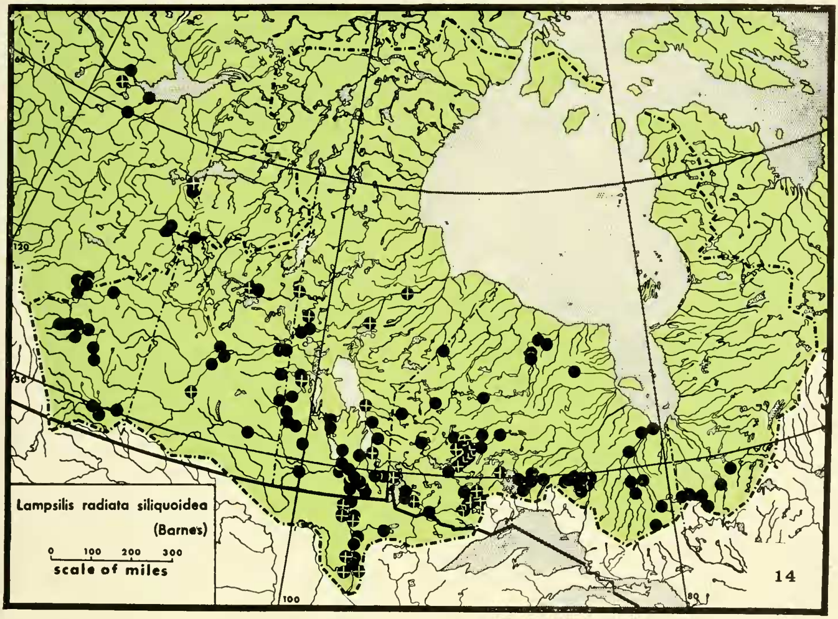
Moose River and Albany River systems. Abundant everywhere. Peripheral records are, Moose River system: Moosonee and Moose Factory, Ont. (both this survey); Albany River system: Stooping River at mouth, 12 mi W of Fort Albany, Ont. (this survey).

Attawapiskat River system. Crow River, Central Patricia, Ont. Attawapiskat River, 4 mi W of Attawapiskat, Ont. (both this survey).

Ekwan River system. Ekwan River, northern Ontario, approximately 100 mi upstream from

TABLE 5. Statistical analyses of populations of *Lampsilis radiata* (*s. lat.*).

Sample	Locality	N	Length, mm	Width/Length	Hp/Hb	Rays	Ecology	
							Water body	Substrate
1	White Earth Creek nr. Smoky Lake, Alta.	24	50·6–(78·4)–119·8	0·269–(0·335)–0·413	1·01–(1·11)–1·20	0–(1·7)–4	r	gs
2	Old Man River nr. Taber, Alta.	14	53·9–(78·5)– 97·0	0·290–(0·342)–0·392	1·02–(1·10)–1·19	1–(1·4)–3	R	m
3	Medicine River, Eckville, Alta.	20	65·5–(78·0)– 98·2	0·310–(0·356)–0·388	1·03–(1·13)–1·23	0–(0·4)–3	—	—
4	Shell River nr. Prince Albert, Sask.	47	61·0–(72·1)– 89·5	0·219–(0·340)–0·373	1·06–(1·14)–1·27	0–(1·6)–4	r	s
5	Red Deer River nr. Hudson Bay, Sask.	18	61·3–(77·6)– 93·9	0·303–(0·351)–0·415	1·02–(1·12)–1·22	0–(1·7)–5	R	gs
6	Qu'Appelle River nr. Welby, Sask.	26	58·1–(81·1)–105·1	0·297–(0·346)–0·398	1·04–(1·12)–1·20	0–(2·2)–5	R	sm
7	Ebb and Flow Lake nr. Kinosota, Man.	10	30·8–(49·4)– 60·1	0·322–(0·357)–0·388	1·04–(1·11)–1·19	0–(0·3)–1	L	c
8	Red River nr. Drayton, N.D.	29	60·2–(80·3)–102·1	0·317–(0·370)–0·461	0·98–(1·11)–1·32	0–(2·4)–5	R	mc
9	Rat River nr. La Rochelle, Man.	30	61·8–(75·0)– 86·5	0·309–(0·349)–0·390	1·09–(1·15)–1·30	0–(1·4)–6	r	sm
10	Red River nr. St. Norbert, Man.	44	58·6–(73·7)– 81·1	0·305–(0·345)–0·383	1·04–(1·10)–1·30	1–(2·6)–6	R	mc
11	Lake Winnipeg nr. Gimli, Man.	25	24·2–(53·9)– 71·2	0·314–(0·402)–0·446	1·06–(1·12)–1·20	0–(1·0)–4	L	s
12	Pelican Lake, Sioux Lookout, Ont.	72	54·0–(74·5)– 88·6	0·312–(0·362)–0·411	1·05–(1·23)–1·42	0–(0·6)–3	L	sm
13	Lake 20 mi E of Beardmore, Ont.	59	64·7–(92·8)–113·7	0·296–(0·344)–0·407	1·09–(1·22)–1·37	0–(0·3)–2	l	sm
14	Pagwachuan River, 75 mi W of Hearst, Ont.	32	54·8–(61·4)– 71·5	0·294–(0·343)–0·377	1·08–(1·21)–1·37	0–(0·3)–3	R	sm
15	Shekak River, 34 mi W of Hearst, Ont.	56	41·7–(58·9)– 69·8	0·309–(0·335)–0·397	1·10–(1·24)–1·38	0–(0·3)–6	R	sm
16	Forde Creek, 25 mi W of Hearst, Ont.	19	60·9–(77·5)– 90·1	0·325–(0·350)–0·382	1·06–(1·14)–1·20	0–(1·2)–4	r	s
17	Driftwood River, 20 mi S of Cochrane, Ont.	14	57·2–(72·6)– 97·0	0·311–(0·343)–0·370	1·08–(1·22)–1·34	0–(2·0)–6	r	s
18	Lake Abitibi, Baie la Sarre, Que.	8	37·8–(68·5)– 94·5	0·339–(0·375)–0·395	1·08–(1·22)–1·35	0–(1·1)–3	L	mc
19	Lac Dubuisson nr. Val d'Or, Que.	13	52·0–(74·3)– 89·1	0·321–(0·365)–0·415	1·13–(1·21)–1·37	0–(1·8)–3	L	c
			Northern Peripheral Populations					
20	Hay River, N.W.T. (60°N, 117°W)	31	22·7–(42·7)– 63·3	0·264–(0·312)–0·356	0·99–(1·06)–1·14	0–(0·3)–1	R	m
21	Winisk River, Ont. (all specimens)	25	54·0–(61·4)– 74·1	0·323–(0·368)–0·407	1·05–(1·17)–1·30	0–(0·9)–5	R	—
22	Moose River, Moose Factory, Ont.	35	41·2–(58·3)– 70·1	0·313–(0·366)–0·420	1·05–(1·15)–1·23	0–(2·3)–6	R	sm



mouth (1965, K. Schiefer!). Ekwan River (1901, D. W. Dowling!).

Winisk River system. Winisk River, northern Ont., at the following localities: 54° 08′N, 87°09′W; 54°23′N, 87°09′W; 54°43′N, 86°30′35″W; and 54°42′N, 86°15′W (all 1903, W. McInnes!). Winisk River, Winisk, Ont. (fragment) (this survey).

Severn River system. Severn Lake, northern end, northwestern Ontario (54°05′N, 90°42′W), North Spirit Lake, Ont., at outlet (52°31′N, 93°02′W) (both this survey). Fawn River, Ont. (54°28′N, 88°16′W) (1967, B. C. McDonald!). Junction of Sachigo and Severn rivers (pers. comm., John Heglund, Big Trout Lake, Ont.).

Hayes River system. Stull Lake, Ont., at outlet (54°29′N, 92°37′W) (this survey).

Winnipeg, Red, and Saskatchewan River systems and Lake Manitoba-Lake Winnipegosis drainage area. Abundant throughout (numerous records.)

Nelson River system. Lake Winnipeg, mouth of Winnipeg River (1883, R. Bell!). Lake Winnipeg, 20 mi S of Gimli, Man. Black River, 24 mi N of Pine Falls, Man. Small Lake, Manigotogan, Man. Stout Lake, Ont., at outlet (52°08′N, 94°44′W) (all, this survey). Pigeon River, Man. (1895, J. B. Tyrrell!). Simonhouse Lake, 46 mi N of The Pas, Man. (this survey). File River Man. (1906, W. McInnes!). Burntwood River, Thompson, Man. (1906, O. O'Sullivan!).

Churchill River system. Churchill River, Sask. (1908, W. McInnes!). Churchill River at Otter Rapids, 54 mi N of La Ronge, Sask. (this survey). Barrington River (56°46′N, 99°44′W), Man. (1966, J. V. Wright!).

Mackenzie River system. Pembina River: near Sangudo, Alta. and near Evansburg, Alta. (both date?, L. S. Russell!). Athabasca River near Lake Athabasca and 75 mi downstream from Waterways, Alta. (2 localities). (1945, J. G. Oughton!). Hay River, 60°N, 117°W, N.W.T. (1964, J. V. Wright!). Great Slave Lake, Hay River Township, N.W.T. (1966, R. W. Coleman!). Hay River at Great Slave Lake, N.W.T. (1919, E. J. Whittaker! and 1966, R. W. Coleman!). Hay River, West Channel, Hay River Township (1966, R. W. Coleman!) Lake Kakisa, west end, 60°55′N, 117°40′W, N.W.T. (Whittaker, 1924: 10). Mackenzie

River, N side of ferry crossing, Highway 3, N.W.T. (1966, R.W. Coleman!). Mills Lake, Mackenzie River, 61°30′N, 118°20′W, N.W.T. (1917, E. M. Kindle!).

Distribution: Mississippi—Missouri system from New York to Arkansas and Minnesota, but absent from the Tennessee River and Cumberland River systems (Ortmann, 1919: 289). Also in the St. Lawrence River system from Lake Superior to Lake Ontario, the upper St. Lawrence River, and the Ottawa River and their tributaries. (In the Lake Ontario and St. Lawrence River region, *Lampsilis radiata siliquoidea* intergrades with *L. radiata radiata* (Gmelin), see Clarke & Berg (1959: 59–61, 68–70)). In the Canadian Interior Basin from Quebec to Alberta and in the Mackenzie River system of Alberta and the Northwest Territories, north to the vicinity of Great Slave Lake.

Biology and Ecology: *Lampsilis radiata siliquoidea* was found in slow to fast moving rivers with widths of 25 to 300 feet and more. It also occurred in lakes whose areas were about 10 acres to those of the largest lakes sampled (e.g., Lake Winnipeg). The bottoms inhabited were of all types (clay, mud, sand, or gravel) and submersed vegetation was abundant, moderately abundant, or sparse. It was often found in water as shallow as 2 or 3 inches deep. This is a shallower depth than that usually occupied by any other unionid. In Quebec *L. r. siliquoidea* ranked behind *Anodonta grandis simpsoniana* and *Elliptio complanata* in abundance. Elsewhere, however, it was ordinarily dominant and was frequently the only unionid species present.

The anatomy of *Lampsilis radiata siliquoidea* has been discussed by Ortmann (1911: 348 under *L. luteola*). During the present survey females with eggs were collected on July 11, 1965 and July 15, 1965 from Qu'Appelle River, Sask., and White Earth Creek, Alta., respectively. Females with apparently mature glochidia were collected from localities in Ontario, Manitoba, and Minnesota from Aug. 3 to Aug. 17 in 1961 and 1965 and also on June 18, 1965 from Blind Man River, Alta. Non-gravid females were collected from July 9 to Aug. 10 in 1961, 1964, and 1965 from several Ontario and Manitoba localities. These data agree in general with those of Ortmann (op. cit.), who states that in Pennsylvania the glochidia are retained from about the first part of August until the middle of the following July. The glochidia are purse-shaped, higher than long, oval, without hooks, and have a straight to slightly curved hinge line. Glochidia from our material measured from $0{\cdot}24 \times 0{\cdot}26$ to $0{\cdot}26 \times 0{\cdot}30$ mm, with some variation in size even among individuals from the same parent.

Coker, *et. al.* (1921: 153) list the following widely distributed fish as hosts for the glochidia of *Lampsilis radiata siliquoidea*:

Bluegill sunfish	*Lepomis macrochirus* Raf.
White crappie	*Pomoxis annularis* Raf.
Black crappie	*P. nigromaculatus* (Le Sueur)
Largemouth bass	*Micropterus salmoides* (Lacépède)
Smallmouth bass	*M. dolomieui dolomieui* Lacépède
White bass	*Roccus chrysops* (Raf.)
Yellow perch	*Perca fluviatilis flavescens* (Mitchill)
Eastern sauger	*Stizostedion canadense* (Smith)
Yellow pikeperch	*S. vitreum* (Mitchill)

Among the fish listed only the *S. vitreum* and *P. fluviatilis flavescens* are known to occur throughout most of

the area occupied by *L. r. siliquoidea* in the Canadian Interior Basin.

Remarks on Nomenclature: Recently Wheeler (1963: 58) has revived the name *Unio luteolus* Lamarck for this subspecies. Her conclusion was based on photographs of Lamarck's type of *U. luteolus* (which resembles some specimens of *Lampsilis radiata siliquoidea*) in the Museum National d'Histoire Naturelle, Paris and on the logical assumption that this specimen probably came from Mohawk River in New York.

Clarke & Berg (1959: 59-68) have shown that in central New York State there is good evidence of widespread gene flow between the eastern *Lampsilis radiata radiata* and the western *L. r. siliquoidea*. Populations in the area of intergradation show much variation and are statistically intermediate between "pure" *radiata* and "pure" *siliquoidea*. Based on present distribution it is probable that the New York State Barge Canal, running from Lake Erie to the Mohawk and Hudson rivers, is the major pathway by which the western *L. r. siliquoidea* has invaded this region in the past 150 years.

The Mohawk River is now polluted throughout much of its length and there are no reports of unionids having been collected from it recently. It is almost certain, however, that if a population of *Lampsilis radiata* was able to exist there it would be similar to other populations from central New York, i.e. intermediate between *L. r. radiata* and *L. r. siliquoidea*. Such populations often contain a few extreme specimens which are of the same appearance as the type of *Unio luteolus* illustrated by Wheeler. It is probable that Lamarck's specimen is such an extreme example from an intermediate population, but a population which in 1819 was even more like *L. radiata* (*s. str.*) than it would be today. because the Barge Canal was not then built. Since we are dealing with populations, not with individual specimens, we must therefore either (1) retain the name *U. siliquoidea* Barnes for the western subspecies and again relegate *U. luteolus* Lamarck (1819) to synonymy under *Mya radiata* Gmelin (1792) (=*Lampsilis radiata radiata* (Gmelin)) or (2) consider *Unio luteolus* a *nomen dubium* because of the uncertainty as to which subspecies its parent population most closely resembled.

As pointed out previously (Clarke & Berg, 1959: 60), *Unio rosaceus* De Kay (*Lampsilis siliquoidea rosacea* etc. of authors) and *Unio borealis* Gray (*Lampsilis borealis* of authors) represent populations which are intermediate between *L. r. radiata* and *L. r. siliquoidea* and are best considered as *L. radiata* (*s. lat.*). *Unio superiorensis* Marsh (*Lampsilis superiorensis* of authors) has, in my opinion, no characters which would justify its recognition as anything but a synonym of *L. r. siliquoidea*.

Remarks on variation: The measurements taken from 22 population samples are summarized in the table under "Measurements." In general, inter-population variation is substantial but is less than that seen in *Anodonta*. Correlations of morphology with geography and ecology are also somewhat more obscure but some relationships do appear to exist.

Geographical Relationships: Sexual dimorphism in shell characters, as indicated by the increased spread of Hp/Hb values, appears to be less in western populations than in eastern. Hp/Hb values are also significantly lower west of the Manitoba-Ontario boundary than east of it. Excluding the 3 northernmost peripheral samples, all 11 western populations show a mean value of 1·15 or less and 7 of the 8 eastern populations show a mean

value of 1·21 or more. Even the 3 northern peripheral populations show this trend although the values of Hp/Hb are all lower. Other characters are not concordant, however, and no taxonomic distinction between the western and eastern populations appears justified.

Growth, as expected, is much slower in northern than in southern populations. The largest specimen in the Hay River sample, for example, is only 63·3 mm long but shows nine growth annuli. Specimens of the same size from more southerly localities (e.g., Red River) often exhibit only 3 growth annuli.

Ecological Relationships: There appears to be a tendency for relative width, as expressed by the ratio W/L to be greater in large lakes than elsewhere (see " Measurements "). The highest mean value (0·402) occurred in the population from the largest lake, Lake Winnipeg. Four of the next 5 highest mean values (excluding northern peripheral populations) were from the 4 other large lake habitats sampled. It is tempting to speculate that this may be a direct result of physical selection. More obese individuals, with their lower surface to volume ratios, might be better able to remain in place without being dislodged by the turbulent and shifting currents which occur in lakes during storms. In rivers with appreciable current it is possible for mussels to orient themselves parallel to the current and this is frequently done. Obese shape may well be a handicap in such an environment and compressed shape may be an advantage.

In general, the largest individuals occurred in rivers, especially rivers close to, and draining, lakes. This is a commonly observed phenomenon in many species of Unionidae.

Water hardness also appears to be a significant factor in this region as elsewhere (see, e.g., Clarke & Berg, 1959: 10). Streams flowing through limestone country often support larger, heavier specimens than are found elsewhere. Conversely, streams flowing through country notably poor in limestone (e.g., Black River, 24 mi N of Pine Falls, Man., Pl. 10, Figs. 4, 5), support only thin shelled, stunted. and frequently dark-coloured individuals.

Lampsilis ovata (Say)

Pocketbook Mussel;
Plate 9, Figs. 1-6; Map 15.

Unio ovatus Say, 1817: *Nicholson's Encyclopedia*, 1st Amer. ed., *2*, pl. 2: 7 (Binney reprint, 1858: 50). Type locality: " Ohio River and its tributary streams."

Lampsilis cardium Rafinesque, 1820: *Ann. Gén. Sci. Phys.*, Brussels, *5* (13): 298, pl. 80: 16–19 (Binney & Tryon reprint, 1864: 43). Type locality: " la rivière Ohio."

Unio ventricosus Barnes, 1823: *Amer. J. Sci.*, *6*: 267, pl. 8: 14. Type locality: " Wisconsin River [and] Mississippi River [at] Prairie du Chien, Wisconsin."

Unio occidens Lea, 1829: *Trans. Amer. phil. Soc.*, *2*: 435, pl. 10: 16. Observations *1*: 128, pl. 10: 16 (1834). Type locality: " Ohio."

Unio canadensis Lea, 1857: *Proc. Acad. natr. Sci. Philad.*, *1*: 85; *J. Acad. natr. Sci.*, *4*: 268, pl. 44: 148 (1860); Observations *7*: 86, pl. 44: 148 (1860). Type locality: " St. Lawrence River, Montreal, Canada."

Lampsilis ventricosa var. *lurida* Simpson, 1914: *Descriptive Catalogue of the Naiades*, etc. p 41. Type locality: " St. Lawrence drainage."

" *Lampsilis ventricosa lurida* Simpson ": Baker, 1928, *Fresh water Mollusca of Wisconsin*, *2*: 289, pl. 93: 5, pl. 94: 5–6.

Lampsilis ventricosa perglobosa Baker, 1928: *Fresh water Mollusca of Wisconsin*, *2*: 285, pl. 93: 1–4. Type locality: " Lake Pepin, near Lake City, Minn."

Lampsilis ventricosa winnebagoensis Baker, 1928: op. cit., p 291, pl. 94: 1–4. Type locality: " Winnebago Lake, near Oshkosh, Wisc."

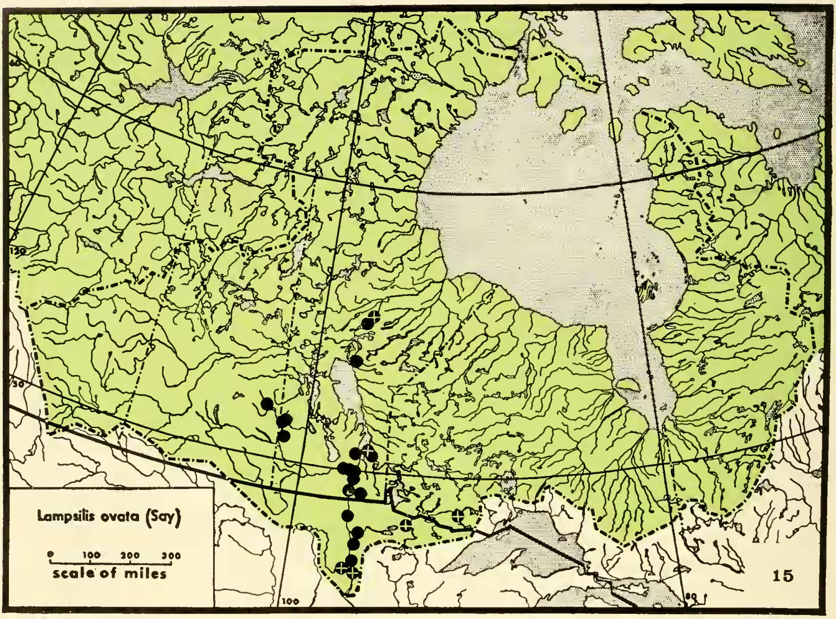
Diagnosis: Shell moderately large, ovate, relatively thick, in most specimens with rays covering the whole surface, and with prominent sexual dimorphism.

Description: Shell fairly large (up to nearly

5 inches long), subelliptical (males) or subovate (females), thickened anteriorly, thinner posteriorly, strong, and inflated. Females typically much higher near the posterior termination of the ligament than at the beaks; males approximately equally high at both points. Periostracum yellowish to olive brown, rather shiny to dull, and typically with narrow to wide dark green rays generally distributed over the entire shell. Rays may be nearly or wholly lacking. Beak sculpture variable, but in most specimens rather coarse and slightly double-looped (Pl. 15, Fig. 16). Pseudocardinal teeth prominent, elevated, conical, compressed, and directed forward, 2 in each valve. Lateral teeth elevated, strong, 1 in the right valve and 2 in the left. Nacre bluish-white or silvery white in all specimens seen from the Canadian Interior Basin. Anterior muscle scars deep, posterior scars and pallial line well-marked.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Red River, 2 mi NE of Drayton, N.D. (males).					
L, mm	9	89·0 —105·7	95·7	—	—
H/L	9	0·596— 0·672	0·631	0·009	0·027
W/L	9	0·369— 0·409	0·389	0·004	0·013
Assiniboine River, western edge of Winnipeg, Man. (males).					
L, mm	26	59·2 —101·4	80·2	—	—
H/L	26	0·622— 0·694	0·656	0·004	0·019
W/L	26	0·370— 0·452	0·406	0·005	0·024
Red River, 2 mi NE of Drayton, N.D. (females).					
L, mm	3	91·1 — 98·6	95·5	—	—
H/L	3	0·689— 0·726	0·705	—	—
W/L	3	0·390— 0·454	0·423	—	—
Assiniboine River, western edge of Winnipeg, Man. (females).					
L, mm	14	67·1 — 89·6	78·1	—	—
H/L	14	0·671— 0·770	0·722	0·009	0·033
W/L	14	0·380— 0·486	0·430	0·009	0·035



Records:

Winnipeg River system. Fern Lake, Rainy River Dist., Ont. (Baker, 1939b: 90); Sturgeon River, Minn. (Dawley, 1947: 679).

Red River system. Red River: 3 mi W of Nielsville, Minn.; Abercrombie, N.D.; 2 mi NE of Drayton, N.D.; St. John Baptiste, Man. (all this survey). Sand Hill River, Climax, Minn. (this survey). Red Lake River, Crookston, Minn. (Univ. Minn.). Little Pine Lake outlet; Otter Tail Lake outlet; and " Red River " [=Otter Tail River] at Perham and below Fergus Falls, Minn. (Wilson & Danglade, 1914: 12). Otter Tail River, Minn.; Sheyenne River, N.D. (both Cvancara, 1967: 189). Roseau River, 8 mi N of Tolstoi, Man.; La Salle River, La Salle, Man.; Assiniboine River: western edge of Winnipeg, Man., 8 mi W of Winnipeg, 12 mi NW of St. Francis Xavier, Man. (all this survey), Millwood, Man. (1888, J. B. Tyrrell!), and 3 mi NE of Amsterdam, Sask. (this survey). Shell River, 6 mi E and 9 mi NNE of Roblin, Man. (this survey).

(?) Saskatchewan River system. Battle River, (Sask.) (Dall, 1905). This record needs confirmation; it is probably incorrect.

Nelson River system. Lake Winnipeg: near Elk Island (mouth of Winnipeg River) (1883, R. Bell!); Victoria Beach (Mozley 1938); and 20 mi S of Gimli, Man. (this survey). Gunisao River, Man. (1895, J. B. Tyrrell!). Nelson River 55°15′N (1906, O. O'Sullivan!) and 55°45′N (Mozley, 1938: 125).

Distribution: Ohio-Mississippi River system from Minnesota to New York and Oklahoma to Tennessee. Potomac River in the Atlantic drainage area (introduced). St. Lawrence River system throughout. Canadian Interior Basin in the Winnipeg, Red, and Nelson River systems.

Biology and Ecology: *Lampsilis ovata* was collected at 13 localities during this survey. Eight of these were in rivers exceeding 100 feet in width, 4 were in rivers 40 to 75 feet wide, and 1 was in a large lake. The larger populations were all from large rivers. Ecological condi-

tions were diverse: vegetation was sparse to medium, current (in the rivers) was slow, moderate, or rapid, and the bottom was of clay, mud, sand, or gravel, with or without rocks. *L. radiata siliquoidea* was dominant in 8 of the 12 river localities. In 3 of the other river localities and in the lake, *Anodonta grandis* was first in abundance and *L. r. siliquoidea* was second, while in the remaining river locality (Red River at Abercrombie, N.D.) 5 species (*Fusconaia flava*, *Amblema plicata*, *Lasmigona complanata*, *Anodonta grandis grandis*, and *Lampsilis radiata siliquoidea*) were about equally abundant.

The anatomy of this species was discussed by Ortmann (1911: 351). The inner edge of the mantle in females has a characteristic ribbon-like flap in front of the branchial opening which may serve to attract host fish during glochidial release (Louise Kramer, pers. comm.). In Pennsylvania, glochidia are held in the female brood pouches from the end of July to near the beginning of the following July. During the present survey, specimens collected in July were without glochidia and those collected in early August (August 4, Red River near Drayton, N.D. and Assiniboine River near Winnipeg, Man.) contained immature glochidia. One specimen from the St. Lawrence River drainage (Trent River, Frankford, Ont.), collected on June 14, 1962, contained mature glochidia which were ovate, with a nearly straight hinge line, without hooks, and measured 0·25 mm wide and 0·30 mm high. This agrees well with Ortmann (1919: 302) who gives $0{\cdot}25 \times 0{\cdot}29$ mm as the dimensions.

Coker *et al.* (1921: 153) report the following fishes as hosts for *Lampsilis ventricosa*: bluegill, *Lepomis macrochirus* Rafinesque; white crappie, *Pomoxis annularis* Rafinesque; largemouth bass, *Micropterus salmoides* (Lacépède); smallmouth bass, *Micropterus dolomieui dolomieui*. Lacépède; yellow perch, *Perca fluviatilis flavescens* (Mitchill); and yellow pikeperch, *Stizostedion vitreum* (Mitchill).

Remarks: Three morphological types occur in this species: (1) the large-stream morph of the Mississippi River drainage area characterized by a sharp posterior ridge and flat to concave posterior slope (morph *ovata s. str.*), (2) the small-stream morph described above (morph *ventricosa*) and (3) the small morph found in lakes (morphs *canadensis* and *lurida*). Typical *ovata* does not occur in the St. Lawrence River or the Hudson Bay drainage area but in the Ohio-Mississippi River system it is commonly found in large, fast-flowing streams. Ortmann (1919: 298, 303) and van der Schalie (1938: 70) have shown quite conclusively that these morphs are not genetically distinct but that they are ecophenotypes. The names *ventricosa* and *canadensis* (with *lurida* as a synonym of *canadensis*) are therefore applicable only at the infrasubspecific level.

I consider *Unio cardium* Raf., and *Unio occidens* Lea to be straightforward synonyms of *Lampsilis ovata* Say. The names *perglobosa* Baker and *winnebagoensis* Baker were proposed for local populations of this variable species (not as true geographic subspecies) and are also of only infrasubspecific value.

Unionidae Erroneously Recorded from the Canadian Interior Basin

Several authors have recorded species from the Canadian Interior Basin which, as a result of the present study and after examination of many museum collections, are now believed not to occur there. These are listed below. Species whose ranges in this area are incorrectly defined (see La Rocque, 1953; Murray & Leonard,

PLATE 9. *Lampsilis ovata*

FIGS. 1, 2. Red River, Aubigny, Manitoba (female) (NMC 14606, 77mm) . . . . p 110.

FIGS. 3, 4. Red River, St. John Baptiste, Manitoba (male) (MNC 30055, 82 mm) . . . . p 110.

FIGS. 5, 6. Assiniboine River, Winnipeg, Manitoba (female) (NMC 14611, 85 mm) . . . . p 110.

PLATE 9

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PLATE 10. *Lampsilis* and *Sphaerium*

FIGS. 1–3. *Lampsilis radiata siliquoidea*, Carrot River, Saskatchewan (NMC 14619; Figs. 1-2, male; Fig. 3, female; both 80 mm) . . . . , ... p 105.

FIGS. 4, 5. *Lampsilis radiata siliquoidea*, Black River, 24 mi N of Pine Falls, Manitoba (NMC 55091, female (?), 60 mm) . . . . p 105.

FIG. 6. *Sphaerium simile*, Wabaskang Lake, 40 mi N of Vermilion Bay, Ontario (NMC 19309, 14 mm) . . . . p 142.

FIG. 7. *Sphaerium simile*, outlet of Off Lake, near Finland, Ontario (NMC 18681, 19 mm) . . . . p 142.

PLATE 10

PLATE 11. *Campeloma*, *Valvata* and *Ferrissia*

FIG. 1. *Campeloma decisum*, Trout Lake, near North Bay, Ontario (NMC 27877, 15 mm) . . . . . p 216.

FIGS. 2, 3. *Ferrissia rivularis*, Crane Lake, Manitoba (NMC 2163, 5·7 mm) . . . . p 479.

FIGS. 4–6. *Valvata sincera helicoidea*, Aberdeen Lake, Northwest Territories (NMC 13265, 5·1 mm) . . . . p 229.

FIG. 7. *Valvata tricarinata* Skunk River near Hearst, Ontario (NMC 13318, 4·3 mm) . . . . . . p 234.

FIGS. 8, 9. *Valvata sincera ontariensis*, Klotz Lake near Longlac, Ontario (NMC 11638, 5·4 mm) . . . . p 225.

PLATE II

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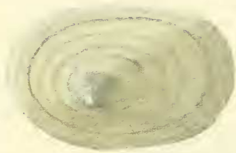

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PLATE 12. *Lymnaea* (1)

FIG. 1. *Lymnaea stagnalis appressa*, Montreal River near Montreal Lake, Saskatchewan (NMC 14814, 51 mm) . . . . p 296.

FIGS. 2, 3. *Lymnaea megasoma* Wild Goose Lake, near Longlac, Ontario (NMC 14822, 38 mm) . . . . p 293.

FIGS. 4–6. *Lymnaea aractica*, Moose River, Moose Factory, Ontario (NMC 19386; 16 mm, 14 mm, 12 mm) . . . . p 319.

FIGS. 7, 8. *Lymnaea catascopium*, Mistassin Lake, northern Ontario (NMC 2202, 15 mm) . . . . p 328.

FIGS. 9, 10. *Lymnaea elodes*, woods pool, Eastmain, Quebec (NMC 19411, 27 mm) . . . . p 351.


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PLATE 13. Physidae and Planorbidae

FIG. 1. *Physa gyrina*, Montreal River near Montreal Lake, Saskatchewan (NMC 14818, 18·0 mm . . . . p 373.

FIG. 2. *Aplexa hypnorum*, swamp near Rocky Mountain House, Alberta (NMC 14819, 12·8 mm) . . . . p 383.

FIGS. 3–5. *Promenetus exacuous exacuous*, Pond at Moose Factory, Ontario (NMC 11498, 4·5 mm) . . . . p 409.

FIGS. 6–8. *Planorbula campestris*, Small Lake 4½ mi W of Hamiota, Manitoba (50 10′N, 100 30′W) (NMC 2322, 10·7 mm) . . . . p 422.

FIGS. 9–11. *Helisoma campanulatum*, (co-type) Bamaji Lake, Ontario (N of Lake St. Joseph) (NMC 4378, 10·0 mm) . . . . p 445.

PLATE 13

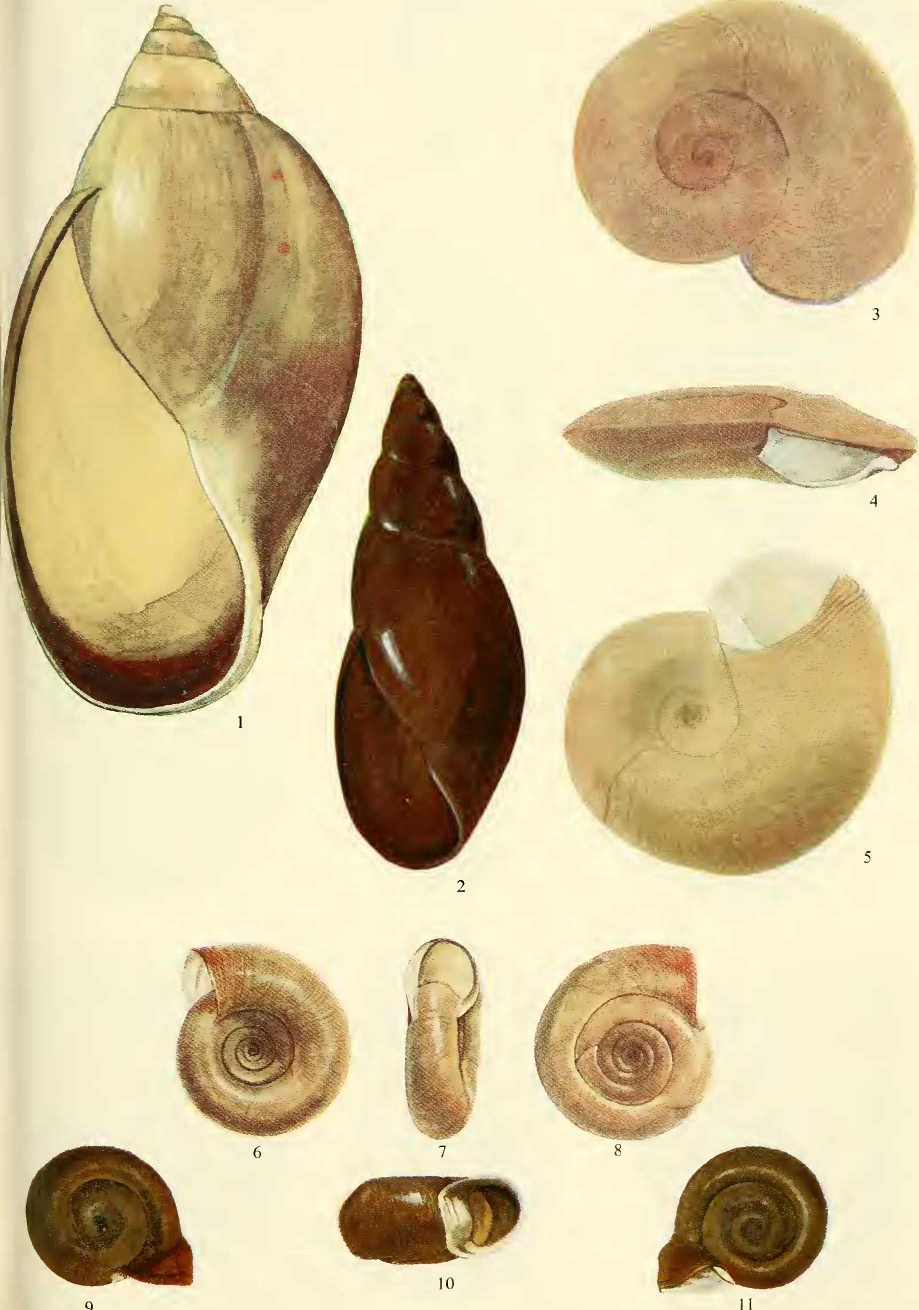


PLATE 14. *Helisoma*

FIGS. 1–3. *Helisoma anceps*, Montreal River near Montreal Lake, Saskatchewan (NMC 19560, 13·7 mm) . . . . p 428.

FIGS. 4–9. *Helisoma trivolvis trivolvis*, Montreal River near Montreal Lake, Saskatchewan (NMC 14815, 19559, 28·7 and 28·0 mm) . . . . p 452.

FIGS. 10–12. *Helisoma pilsbryi infracarinatum*, Basswood River Rapids, Ontario-Minnesota International Boundary (NMC 3222, paratype of *H. infracarinatum* Baker, 22·9 mm) . . . . p 459

PLATE 14

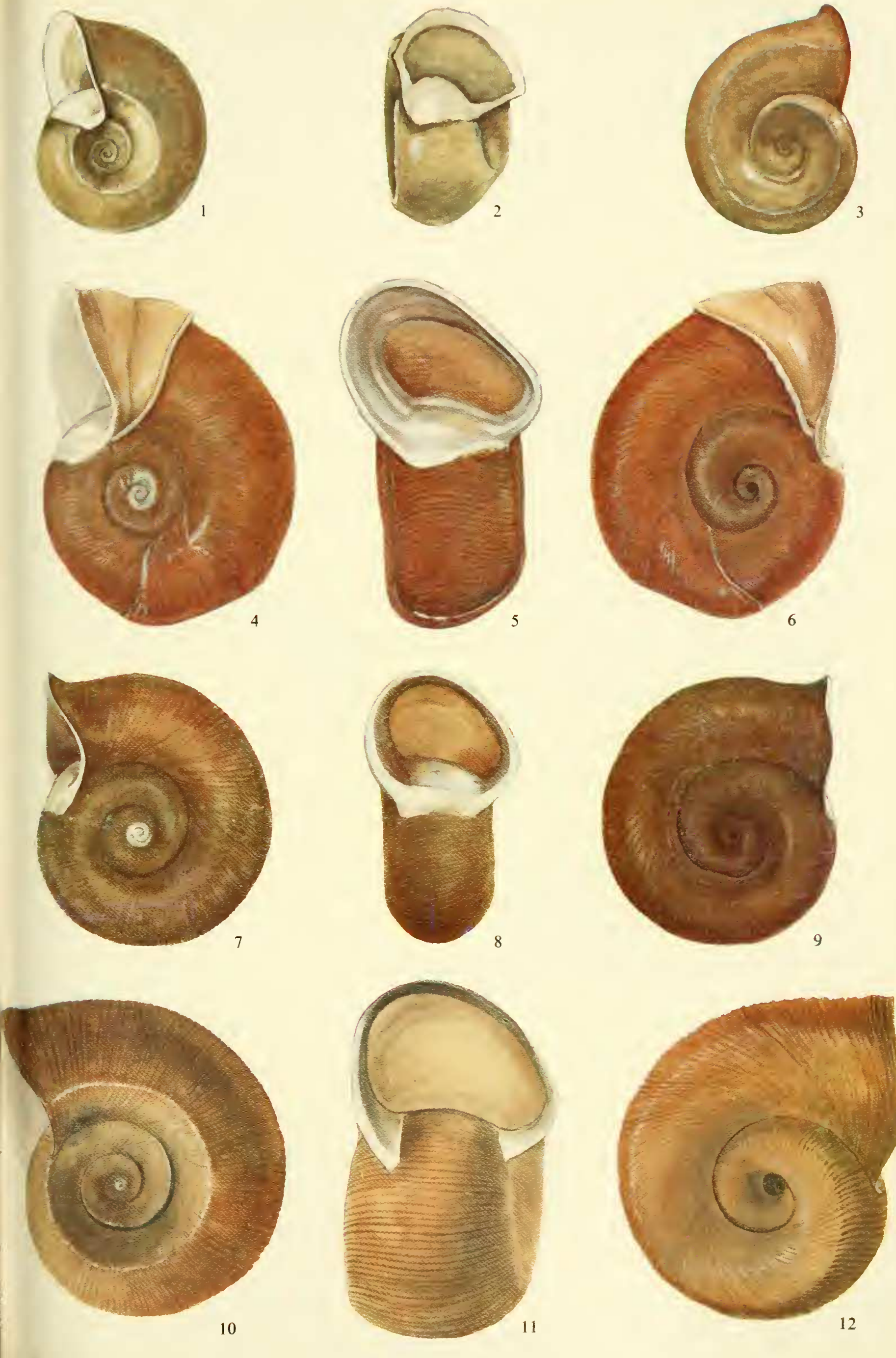
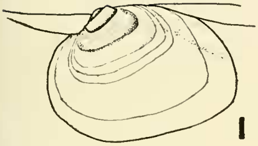


PLATE 15. Unionidae beak sculpture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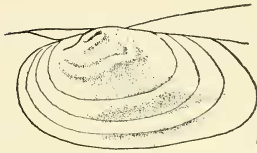
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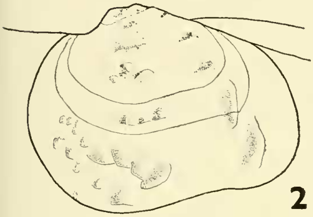
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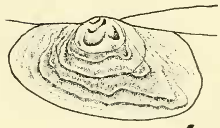
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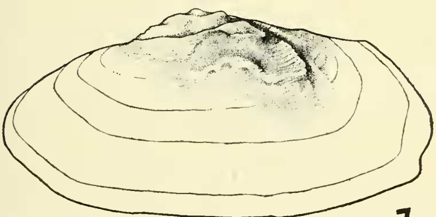
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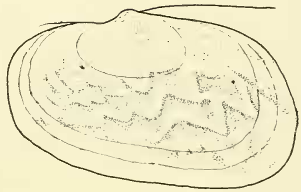
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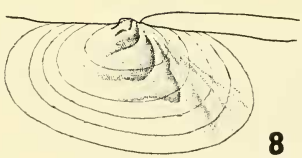
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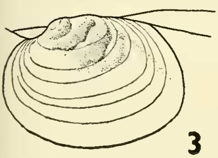
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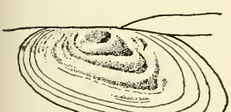
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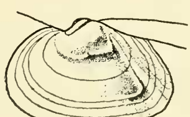
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PLATE 16. *Sphaerium*

FIG. 1. *Sphaerium striatinum*, Birdtail River, Riding Mountain, Manitoba (NMC 5970, 14 mm) . . . . p 145.

FIG. 2. *Sphaerium rhomboideum*, Sturgeon Lake Saskatchewan (NMC 17939, 12 mm) . . . . . p 138.

FIG. 3. *Sphaerium transversum*, Playgreen Lake, Manitoba (NMC 1854, 8·1 mm) . . . . p 160.

FIG. 4. *Sphaerium occidentale*, swamp at Moose Factory, Ontario (NMC 14767, 7·4 mm) . . . . . p 149.

FIG. 5. *Sphaerium lacustre* (*ryckholti* morph), 19 mi SW of Turner Valley, Alberta (NMC 19284, 7·5 mm). . . . . p 154.

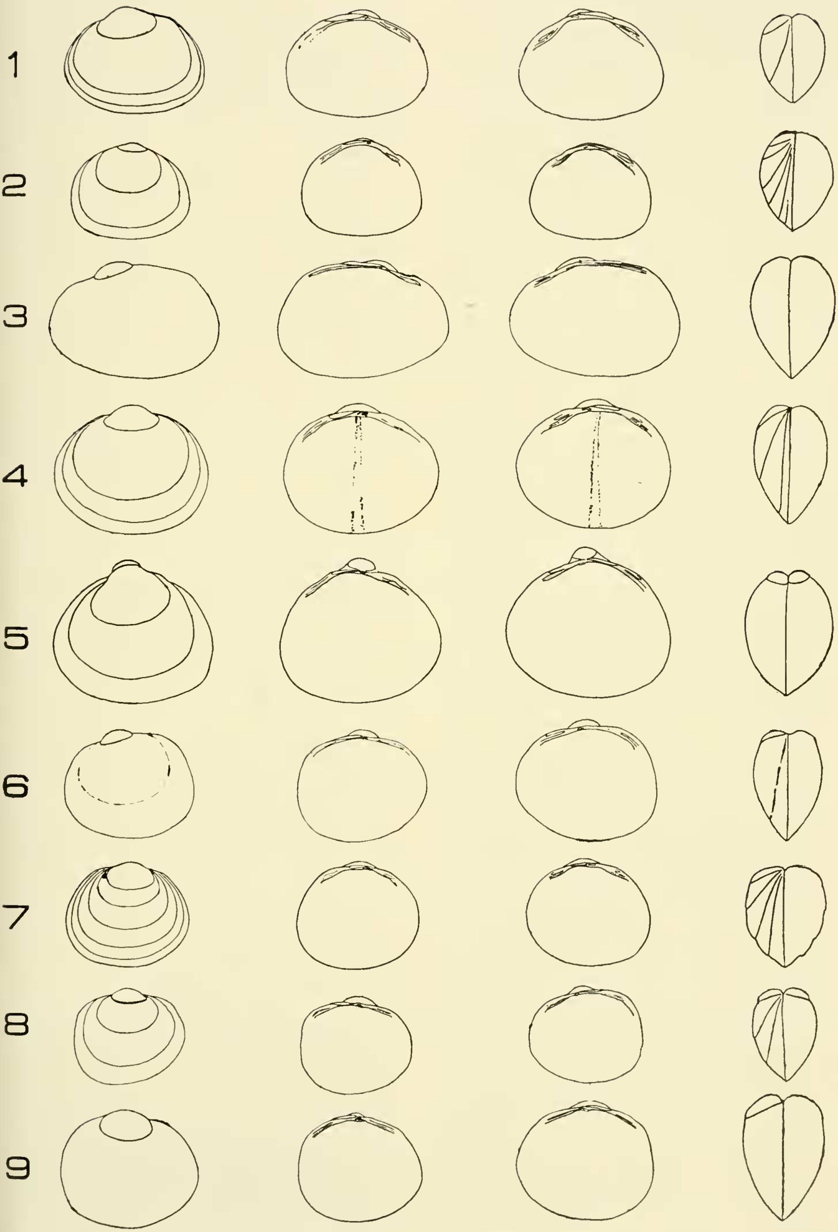
FIG. 6. *Sphaerium partumeium*, Salmon River at Roblin, Ontario (NMC 17088, 6·2 mm). . . . p 155.

FIG. 7. *Sphaerium nitidum*, Aberdeen Lake, Northwest Territories (NMC 15536, 5·9 mm) . . . . p 135.

FIG. 8. *Sphaerium securis*, Napanee River above Petworth, Ontario (NMC 5831, 5·4 mm) . . . . p 157.

FIG. 9. *Sphaerium lacustre*, (typical morph) Klotz Lake near Longlac, Ontario (NMC 19137, 3·2 mm) . . . . p 152.

See also Plate 10, figs. 6, 7. (*S. simile*).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1962, etc.) but which do occur in the region are discussed elsewhere. Species names which have been synonymized in the present work are listed in the index and are not included below.

Margaritifera margaritifera (Linnaeus). Reported by Dall (1905: 132) from " the Lower Saskatchewan near Lake Winnipeg. " The specimens on which this record is based are not in the United States National Museum and could not be found elsewhere. It is most unlikely that *M. margaritifera* would occur at that locality and Dall's record is believed to be based on mislabelled material. Dall's record of *Elliptio complanata* from the Saskatchewan River (op. cit., p 133), which is also probably erroneous, may have been based on the same wrongly labelled collection.

Megalonaias gigantea (Barnes). Reported by Dall (1905: 133, as *Quadrula heros* Say) from " Red River of the North, Manitoba." This and other such records have been repeated by subsequent authors. No specimens of *M. gigantea* from the Red River have been seen and the record is believed to be based on misidentified, large specimens of *Amblema plicata* (Say).

Anodonta implicata Say. Reported by Dall (1905: 129) from " Manitoba in Lake Winnipeg, and Souris River: lower Saskatchewan River." Dall's specimens are in the United States National Museum (USNM 128768, 128775) and are actually *Anondonta grandis grandis* Say.

Obliquaria reflexa (Rafinesque). Reported by Dawley (1947: 692) from the Red River. Also shown by Murray & Leonard (1962: 104, on inset map) as occurring throughout nearly all Ontario. The Dawley collections and other material on which she based her report at the University of Minnesota do not contain that species. Dr. Dawley has informed me (pers. comm. Sept. 3, 1966) that she included this species on the basis of a specimen labelled " Pembina, N.D., 1941 " but her records do not show the identity of the collector. *O. reflexa* was not found during the present survey. In Canada it is known only from the extreme southern tip of Ontario in the Lake St. Clair and Lake Erie drainage areas (La Rocque & Oughton, 1937: 153).

Actinonaias carinata (Barnes). Reported by Dall (1905: 126, as *Lampsilis ligamentinus* Lamarck) from " Roseau River and Millwood, Assiniboine River, Man. " Also reported by Mozley (1938: 125) from " Assiniboine River at Treesbank, Man. " and by Dawley (1947: 692) from the Red River and the Sturgeon River in Minnesota. The specimens reported by Dall and by Mozley have not been found, but Dawley's specimens from Sturgeon River, in the Department of Zoology, University of Minnesota, are *Lampsilis ovata* Say. It is probable that all records of *A. carinata* from the Canadian Interior Basin are based on *L. ovata*. Some male specimens of *L. ovata* resemble *A. carinata* quite closely. Shells of *A. carinata* are thickened and flattened centrally, however, whereas those of *L. ovata* are not and the hinge teeth of the two species are also different.

Actinonaias ellipsiformis (Conrad). Reported by Dall (1905: 126, as *Lampsilis ellipsiformis*) from " Red River of the North [and] Lake Winnipeg, Man. " No specimens of this species were seen during the present survey or in museum collections from this region and these records have not been substantiated by any subsequent author. These records also are probably based on misidentifications of *Lampsilis ovata*.

Leptodea fragilis (Rafinesque). Reported by Dall (1905: 127, as *Lampsilis gracilis* Barnes) from " Red River of the North. " No specimens were seen from the Red River or its tributaries during this survey and it was not reported from there by Dawley (1947). I have collected it in the Minnesota River at Montevideo, Minn.

(Mississippi River system) not far from the Red River system. Perhaps the record was based on juvenile specimens of *Properta alata* (Say) or of *Lasmigona complanata* (Barnes), although the resemblance of these species to *Leptodea fragilis* is only remote.

Carunculina parva (Barnes). Shown by Murray & Leonard (1962: 136, on inset map) as occurring in southern Manitoba and western Ontario. This is probably based on Baker's (1928b: 253) vague record "southern Canada." It is at present known in Canada only from Lake Erie and its tributaries. The University of Minnesota has a specimen from Big Stone Lake, Minn. This lake is within a few miles of the headwaters of the Red River but it is part of the Mississippi River system.

Superfamily Sphaeriacea

The Sphaeriacea are subovate or subtriangular with porcelanous shells and lateral hinge teeth both anterior and posterior to the cardinal teeth. They are found in freshwater and in brackish water and are world-wide. The young are held in the mantle cavity during juvenile growth and, in contrast to Unionidae, no parasitic stage occurs. Three families are recognized (following Thiele, 1935), viz., Corbiculidae, Cyrenoididae, and Sphaeriidae, but only the last named lives in boreal and arctic North America.

Family SPHAERIIDAE Jeffreys

Cycladidae Rafinesque, 1820 (original orthography: Cycladia). *Ann. Gén. Sci. Phys.*, Brussels, *5*(13): 318 (Binney & Tryon reprint, 1864: 61). Type Genus *Cyclas* Lamarck, 1798 [=*Sphaerium* Scopoli 1777]. Cycladidae is a *nomen oblitum.*

Pisidiidae Gray (*in* Turton), 1857 (original orthography: Pisidiadae). *Manual of the land and fresh water shells of the British Islands*, p 263. Type genus *Pisidium* Pfeiffer. Pisidiidae Gray has been placed on the Official List of Family-Group names in Zoology (Name No. 36) "for use by any worker who may consider that the genera *Pisidium* Pfeiffer and *Sphaerium* Scopoli. 1777, the type genus of the taxon Sphaeriidae, belong to different family-group taxa" (Direction 27).

Sphaeriidae Jeffreys, 1862. *Br. Conchol.*, *1*: 1. Type Genus *Sphaerium* Scopoli (1777). According to the ICZN Rules, Article 40, Sphaeriidae Jeffreys must date from Cycladidae Rafinesque (1820) which is the earliest family-group name applicable to this group. As such Sphaeriidae Jeffreys has priority over Sphaeriidae Erichson (1845 Insecta). A proposal to place Sphaeriidae Jeffreys on the Official List of Family-Group Names in Zoology, and to amend Sphaeriidae Erickson to Sphaeridae, is now pending (ICZN).

Shell small to minute (less than 1 inch long); subovate, subrhomboid, or subtriangular, ligament short and delicate; pallial line simple and indistinct, lateral teeth moderately long, placed both anteriorly and posteriorly to the umbones with both sets double in the right valve and single in the left; cardinal teeth small, located between the lateral sets in each valve, generally single in the right valve and double in the left, although left-right reversal of hinge teeth is occasionally seen.

Anatomically the Sphaeriidae are rather similar to the Unionidae. They are all hermaphroditic and ovoviviparous, however, and at least some are autogamic. The young are not parasitic but are free-living and often quite large when they leave the parent. Sphaeriidae are phytophagous filter-feeders. Herrington (1962) has reduced the number of recognized North American species of Sphaeriidae to 35. The total number of Recent species in the world is probably of the order of 100. Geologic range: Upper Jurassic (?) or Lower Cretaceous to Recent.

For details of sphaeriid anatomy, reproduction and growth, see Drew, 1896; Gilmore, 1917; Odhner, 1929; Ellis, 1940; Thomas, 1959; Herrington, 1962; and Heard, 1963a and 1965.

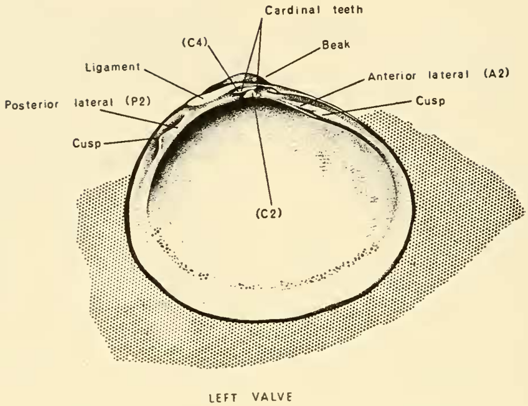


FIG. 5. Interior morphology of the left valve of a *Pisidium* shell.

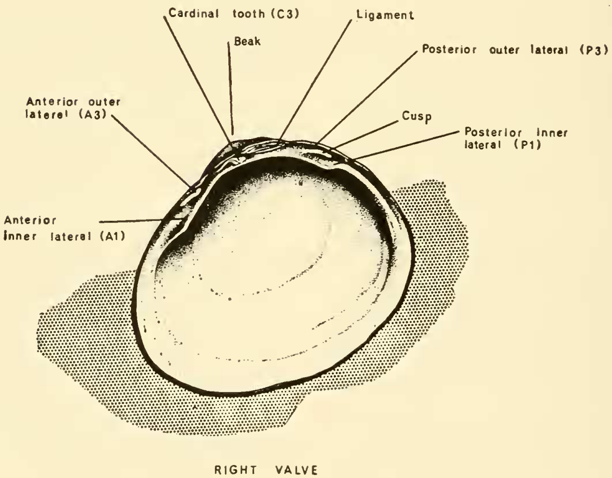


FIG. 6. Interior morphology of the right valve of a *Pisidium* shell.

The specimens reported in this section have all been identified or have had their identifications verified by H.B. Herrington.

Herrington's fine revision of the Sphaeriidae (1962) was also drawn upon liberally viz., the most commonly used synonyms and the descriptions of most of the species

are taken from that work. The taxonomic key, although revised by me, is also based on the key in Herrington's revision. The remainder of the text, etc., unless otherwise noted, is my own work.

The procedure followed under " Measurements " for all species is the same as that used by Herrington (1962) except where the number of specimens was insufficient, i.e., a graded series of 13 specimens was selected which approximate the size variation seen in the lot and specimens 1, 5, 9 and 13 were measured. Width (W) is maximum distance between the outer surfaces of both valves with valves appressed. All dimensions are in millimetres unless otherwise specified.

A comment regarding Herrington's use of " parallel " is necessary. Throughout his work Herrington uses the word to mean curved in the same manner, but not necessarily in the same direction. For example under *Pisidium casertanum* (P 33) he says " dorsal and ventral margins parallel. " These margins are both evenly curved and have approximately the same degree of arc but they are curved in *opposite* directions.

KEY TO THE SPECIES OF SPHAERIIDAE*

1. Umbones anterior or, if subcentral, on the anterior side of centre. Length 5–25 mm (*Sphaerium*) 2
   Umbones posterior or, if subcentral, on the posterior side of centre. Length 2–12 mm (*Pisidium*) 12

2. Shell relatively thick and strong; sculptured with coarse threads or striae (8 or fewer per mm in the middle of the shell) 3
   Shell relatively thin and (in many cases) fragile; sculptured with fine threads or striae (12 or more per mm in the middle of the shell) 4

3. Threads or striae evenly spaced. Length of many adults exceeding 16 mm. Juveniles with dorsal margin nearly straight . . . . . *Sphaerium simile* (p 142, Pl. 10, Figs. 6, 7)
   Threads or striae unevenly spaced. Length of adults less than 16 mm. Juveniles with dorsal margin curved . . . . *Sphaerium striatinum* (p 145, Pl. 16, Fig. 1)

4. Shell elongate in lateral outline, height less than 3/4 of the length . . . . *Sphaerium transversum* (p 160, Pl. 16, Fig. 3)
   Shell less elongate, heigth more than 3/4 of length 5

5. Shell rounded ventrally, anteriorly, and posteriorly, umbones centrally located 6
   Shell rounded or slightly flattened ventrally, rounded anteriorly, subtruncate or shallow convex posteriorly, and with umbones anterior of centre or subcentral 7
   Shell flattened ventrally, subtruncate anteriorly and posteriorly, and with umbones slightly anterior of centre or subcentral 11

6. Threads or striae similar in height and spacing over the whole surface, including the umbones. No radial ridge in middle and inside of valves. Habitat: subarctic or, if farther south, in deep, cold water. . . . . *Sphaerium nitidum* (p 135, Pl. 16, Fig. 7)
   Threads or striae poorly developed or absent in the umbonal region. Low radial ridge in middle and inside of valves. Habitat: swamps, ditches, and vernal ponds . . . . . *Sphaerium occidentale* (p 149, Pl. 16, Fig. 4)

7. Length of some specimens exceeding 7 mm 8
   Length never exceeding 7 mm 9

8. Dorsal margin nearly straight, ventral margin rounded, striae fine and closely spaced (approximately 30 per mm or more) . . . . *Sphaerium partumeium* (p 155, Pl. 16, Fig. 6)
   Dorsal margin curved, ventral margin broadly curved but not rounded**, striae coarser

* The anterior and posterior of empty shells can be found by examination of the hinge teeth. The right valve bears a single cardinal tooth and 4 (2 pairs) of lateral teeth and the left valve bears 2 cardinals and 2 single laterals. In life the animal moves forward with the umbones held upward. See text Figs. 5 and 6 for definitions of structural names in Sphaeriidae.

** Except in *S. lacustre* morph *ryckholti*, which has a rounded ventral margin.

and more widely spaced (approximately 25 per mm or fewer) · · · · · · · · · · ·
Sphaerium lacustre (p 152, Pl. 16, Fig. 9)

9. Umbones elevated and calyculate (capped) · 10
Umbones depressed and not calyculate
Sphaerium nitidum (p 135, Pl. 16, Fig. 7)

10. Umbones centrally located, shell surface dull to glossy, striae rather coarse and not closely spaced (fewer than 20 per mm)
Sphaerium securis (p 157, Pl. 16, Fig. 8)
Umbones located centrally or anterior of centre, shell surface glossy, striae fine and closely spaced (more than 25 per mm)
Sphaerium partumeium (p 155, Pl. 16, Fig. 6)

11. Umbones prominent and distinctly elevated above hinge line. Shell subtrapezoid . . . . .
Sphaerium lacustre (p 152, Pl. 16, Fig. 9)
Umbones not prominent and only slightly elevated. Shell subrhomboid . . . . . · · · · · · · · · · · · · · · · · · · *Sphaerium rhomboideum* (p 138, Pl. 16, Fig. 2)

12. Shell large, adult specimens exceeding 6 mm in length, common · · · · · · · · · · · 13
Shell medium-sized to small, adult specimens less than 6 mm in length · · · · · · · · 15

13. Shell long in lateral outline, height less than 85% of length; cusp of P2 on distal side of centre · · · · · · · · · · · · · · · · · · 14
Shell higher in lateral outline, height of most specimens approximately 90% of length; cusp of P2 central · · · · · · · · · · · · ·
Pisidium idahoense (p 166, Pl. 17, Fig. 1)

14. Periostracum moderately dull to slightly glossy. C4 longer than C2 · · · · · · · ·
Pisidium casertanum (p 171, Pl. 17, Figs. 3, 4)
Periostracum very dull. C4 about the same length as C2 · · · · · · · · · · · · · · · ·
Pisidium adamsi (p 169, Pl. 17, Fig. 2)

15. Anterior cusp of left valve twisted toward the interior · · · · · · · · · · · · · · · · ·
Pisidium fallax (p 179, Pl. 18, Fig. 2)
Anterior cusp of left valve not twisted but parallel to the dorsal margin · · · · · · 16

16. Ventral edge of shell markedly truncate in end view · · · · · · · · · · · · · · · · · ·
Pisidium milium (p 186, Pl. 18, Fig. 5)
Ventral edge of shell tapering, not truncate in end view · · · · · · · · · · · · · · · 17

17. Hinge long (more than 3/4 shell length) · 18
Hinge short (less than 3/4 shell length) · 25

18. Cardinal teeth central or subcentral 19
Cardinal teeth near anterior cusps 24

19. In most specimens, shell shaped like a parallelogram, i.e., anterior and posterior ends sloped at the same angle. Arctic and subarctic and, when farther south, in cold water of large lakes · · · · · · · · · · . · · · ·
Pisidium conventus (p 209, Pl. 19, Fig. 6)
Anterior and posterior ends sloped at different angles, not parallel · · · · · · · · · · · 20

20. Shell surface dull, not glossy · · · · · · · 21
Shell surface glossy · · · · · · · · · · · · 22

21. Shell with straight or slightly curved ridges on the umbones · · · · · · · · · · · · · ·
Pisidium compressum (p 174, Pl. 17, Fig. 5)
Shell without ridges on the umbones . . . . .
Pisidium punctatum (p 212, Pl. 19, Fig. 7)

22. Umbones prominent; shell surface with striae moderately close together (fewer than 30 striae per mm) · · · · · · · · · · · · · · · 23
Umbones not prominent; shell surface with striae close together (more than 30 striae per mm) and, in many specimens, with several coarse striae at the outer edge of the embryonic shell · · · · · · · · · · · ·
Pisidium nitidum (p 190, Pl. 18, Fig. 6)

23. Umbones subcentral · · · · · · · · · · · · ·
Pisidium equilaterale (p 177, Pl. 18, Fig. 1)
Umbones located posterior-dorsally . . . . .
Pisidium variabile (p 197, Pl. 19, Fig. 2)

24. Cusp of A2 toothpick-shaped, i.e., with nearly vertical and parallel sides · · · · · · · · ·
Pisidium ferrugineum (p 181, Pl. 18, Fig. 3)
Cusp of A2 not toothpick-shaped, but with steeply inclined sides · · · · · · · · · · · ·
Pisidium casertanum (p 171, Pl. 17, Figs. 3, 4)

25. Cusp of P2 central or on proximal side of centre · 26
Cusp of P2 distal or on distal side of centre · 28

26. Surface glossy and finely striate (more than 30 striae per mm) · · · · · · · · · · · · 27
Surface dull and moderately striate (fewer than 30 striae per mm) · · · · · · · · · ·
Pisidium walkeri (p 203, Pl. 19, Fig. 5)

27. Anterior (proximal) end of posterior sulcus (i.e., the indented area between the lateral teeth) in right valve closed by a pseudocallus ·
Pisidium ventricosum (p 200, Pl. 19, Figs. 3, 4)
Anterior (proximal) end of posterior sulcus in right valve not closed · · · · · · · · ·
Pisidium subtruncatum (p 194, Pl. 19, Fig. 1)

28. Anterior end of shell joining dorsal margin at an angle · · · · · · · · · · · · · · · · · · *Pisidium lilljeborgi* (p 182, Pl. 18, Fig. 4)
    Anterior end curving gently into the dorsal margin · · · · · · · · · · · · · · · · · · · 29
29. Dorsal margin almost straight or only slightly curved · · · · · · · · · · · · · · · · · · · *Pisidium casertanum* (p 171, Pl. 17, Figs. 3, 4)
    Dorsal margin well rounded · · · · · *Pisidium ventricosum* (p 200, Pl. 19, Figs. 3, 4)

Genus *Sphaerium* Scopoli

Sphaerium Scopoli, 1777: *Introductio ad Historiam Naturalem* [etc.], p 397. Type species: *Tellina cornea* L., by monotypy. *Sphaerium* Scopoli has been placed on the Official List of Generic Names in Zoology (ICZN, Opinion 94, 1926).

Cyclas Lamarck, 1799: *Mém. Soc. Hist. natr. Paris*, p 84. Type species: *Tellina cornea* L., by monotypy.

Amesoda Rafinesque, 1820: *Ann. Gen. Sci. Phys.*, Brussels, *5*(13): 219. (Binney & Tryon reprint, 1864: 61). Type species: *Cyclas similis* Say, by subsequent designation (Baker, 1928b: 312), *Amesoda* is thereby available for the *S. simile* —*S. striatinum* group (W. H. Heard, pers. comm.).

Shells small (5 mm) to medium-sized (25 mm), subovate to subrhomboid, and with umbones located centrally or anterior of center. A distinct anal siphon and a distinct branchial siphon are both present but they are fused either basally or for most of their length. Four gills are present, 2 on each side, and the inner (pericardial) nephridial tube is looped in an anterio-basal direction.

A cosmopolitan genus. "Fingernail clams" occur abundantly in lakes, ponds (perennial and vernal) and streams and are important in the diet of many fishes. Twelve species are recognized by Herrington (1962) as occurring in North America and nine of these, belonging to 3 subgenera, are found in the Canadian Interior Basin. Geologic range: Upper Jurassic(?) or Lower Cretaceous to Recent.

Subgenus *Sphaerium* Scopoli (*s. str.*)

Adult specimens from about 8 to 25 mm in length, shell walls moderately thick and strong, striae coarse to moderately fine, shells rounded posteriorly, and without a low, internal, radiating rib. Umbones not calyculate, i.e., not "capped". Embryonic young within a single adult number up to about 17 and are predominantly of different sizes (in the material examined). Habitat: in perennial water bodies.

Seven species are now recognized from North America but 3 (*Sphaerium corneum* (L), *S. fabale* Prime, and *S. patella* Gould) do not occur in our area. Geologic range: Upper Jurassic (?) or Lower Cretaceous to Recent.

Sphaerium (*Sphaerium*) *nitidum* Clessin

Plate 16, Fig. 7; Map 16.

Sphaerium tenue (Prime) of authors (e.g., Mozley, 1938: 119) but probably not *Cyclas tenue* Prime, 1852. See Herrington, 1948b: 10 and Johnson, 1959: 475.

Sphaerium nitidum Clessin (*in* Westerlund), 1876: Neue Binnenmollusken aus Sibirien. *Nachrichtsbl. deut. malakozool. Ges.*, *8*: 102. Type locality: "in Sibiria prope Jenissei ad Sargutskoj (Lat. 68° 50′)."

Diagnosis: Shell up to about $\frac{1}{3}$ inch long, fragile, evenly ovate, with low umbones and rather fine striae covering the whole outer surface.

Description: "Shell small, considerably inflated, walls very thin, somewhat spherical in outline; beaks about central, low; striae moderately fine, uniformly spaced and maintaining their size right up over the beaks; periostracum a dull gloss;...hinge short, narrow, and only slightly widening at cusps; cusps all distal, moderately sharp on top; cardinals near anterior cusps; hinge-plate very narrow with all the cardinals slim and rather faint...*Sphaerium nitidum* has roughly the appearance of a small, well-inflated *S. corneum*." (Herrington 1962: 21).

Measurements:

Spec. No.	L	H	H/L	W	W/L
Klotz Lake, 30 mi E of Longlac, Ont.					
1	3·7	3·9	1·05	3·7	1·00
5	3·1	2·9	0·94	3·0	0·97
9	2·9	2·7	0·93	2·8	0·97
13	2·3	2·0	0·87	2·2	0·96
Sturgeon Lake, Sask. (53°25′N, 106°06′W).					
1	6·0	5·2	0·87	4·4	0·73
5	5·3	4·9	0·92	3·8	0·70
9	5·0	4·2	0·84	3·3	0·66
13	3·8	3·1	0·82	2·5	0·66
Vaillant Lake, N.W.T. (66°13′N, 114°30′W).					
1	5·7	4·9	0·86	3·6	0·63
5	4·9	4·0	0·82	2·9	0·59
9	4·0	3·3	0·82	2·3	0·58
13	2·9	2·3	0·79	1·5	0·52

Records:

The localities for the 75 collections of *Sphaerium nitidum* from the research area are plotted on Map 16 and only marginal records are given below.

Quebec. Rivière du Gué (57°10′N, 70°35′W). Lac Aigneau (57°10′N, 70°35′W) (both 1955, D. R. Oliver!). Kikkerteluk River, 8 mi E of mouth (58°00′N, 77°02′W) (this survey).

Ontario. Klotz Lake, 30 mi E of Longlac (see "Remarks"). Lake, source of Shell Brook (55°20′N, 87°17′W) (both this survey).

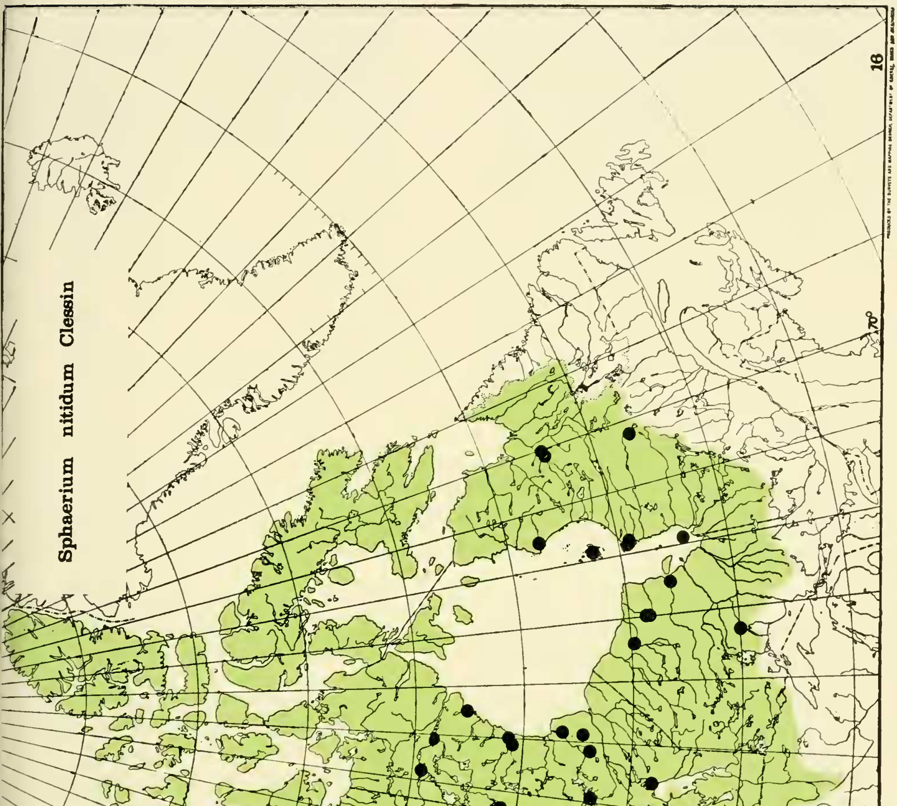
Manitoba. Traverse Bay, near Victoria Beach, Lake Winnipeg (Mozley, 1938: 119).

Saskatchewan. Sturgeon Lake (53°25′N, 106°06′W) (1955, D. S. Rawson!).

Northwest Territories. Aberdeen Lake (64°35′N, 100°00′W) (Elizabeth Macpherson!). Keyhole Lake, Victoria Island (69°22′N, 106°14′W) (1965, Fish. Res. Bd.!). Parry Peninsula (69°27′N, 124°30′W) (1962, Fish. Res. Bd.!). Small Lake near Mackenzie River mouth (69°22′N, 133°36′W) (1957, Fish. Res. Bd.!).

Distribution: Northern Maine and all the Great Lakes (except Lake Erie) north in the boreal forest region and beyond to northern Ungava and Victoria Island, west to Washington and the Aleutian Islands and south in the Rocky Mountains to Utah (Herrington 1962: 21 and this work). It also occurs across northern Eurasia (see Odhner 1939: 80).

Biology and Ecology: Most of the specimens of this species were collected from the stomachs of whitefish caught in Northwest Territories lakes, chiefly by the Fisheries Research Board. Of the 13 lots collected during this survey, nine are from large lakes, one is from a small lake (Owl Lake, Man.) and three are from large rivers. Vegetation was moderate to sparse at most localities,


Sphaerium nitidum Clessin
18
70°
100°

bottom sediments were of all types, and in lotic habitats current was slow to moderate. One locality (Klotz Lake, Ont.) had dense vegetation and is anomalous — see " Remarks."

The anatomy of *Sphaerium nitidum* has been discussed by Odhner (1929: 42). It is rather similar to *S. corneum* except for the relative size of some organs, e.g., the gills of *S. nitidum* are larger.

Six adult specimens from McVicar Arm, Great Bear Lake, N.W.T. collected by the Fisheries Research Board on August 20, 1965 were examined* for shelled young, with the following results:

Adult Length, mm	No. of Young	Length of Young, mm
6·9	1	1·2
6·0	2	1·9 (2)
5·8	6	2·1, 2·0 (3), 1·9 (2)
5·7	2	2·3, 0·5
5·5	1	1·1
5·4	3	1·1 (3)

* In *S. nitidum* and in the other species of *Sphaerium* (*s. lato*) only the unborn, shelled young (i.e. prodissoconch and extra-marsupial stages), as determined by dissection, were measured and counted. In some instances the absence of larval shells may have been a result of dissolution by the preservative so only those young exceeding 0·5 mm in length were recorded.

Six specimens from other arctic localities were also examined and from 0 to 5 young, mostly of different sizes were found in each. Small juveniles, i.e., those about 1 mm long or less, are often of the same size in a single parent but larger juveniles appear to be usually of slightly different sizes.

Remarks: *Sphaerium nitidum* is a cold-water species typically occurring only in deep or unusually cold water bodies in the southern part of its range. Growth rests are prominent and appear as dark, concentric bands, and growth rests are often accompanied by inward contraction of the shell margin. In some populations these contractions are so prominent that the shell surface, viewed in profile, resembles a convex flight of stairs.

One population, that from Klotz Lake, 30 mi E of Longlac, Ont. deserves special comment. Adult specimens are extremely inflated and some are nearly globular (see " Measurements "). Klotz Lake appears to be much too eutrophic to be suitable for this subarctic sphaeriid, especially since it is there close to the southern edge of its range. The lake also supports a large number (35) of other freshwater molluscan species, including *Valvata sincera ontariensis*, a subspecies apparently poorly adapted for interspecific competition.

This population of *Sphaerium nitidum* may well deserve subspecific status but a fuller investigation of variation within this species should precede any such decision.

Sphaerium (*Sphaerium*) *rhomboideum* (Say)
Plate 16, Fig. 2; Map 17.

Cyclas rhomboidea Say, 1822: *J. Acad. natr. Sci. Philad.*, *2*: 380 (Binney reprint, 1858: 111). Type locality: " Lake Champlain."

Diagnosis: Shell up to about ½ inch long, thin walled but fairly strong, rounded dorsally, flattened ventrally, with sub-

truncated ends, and with low, centrally located umbones.

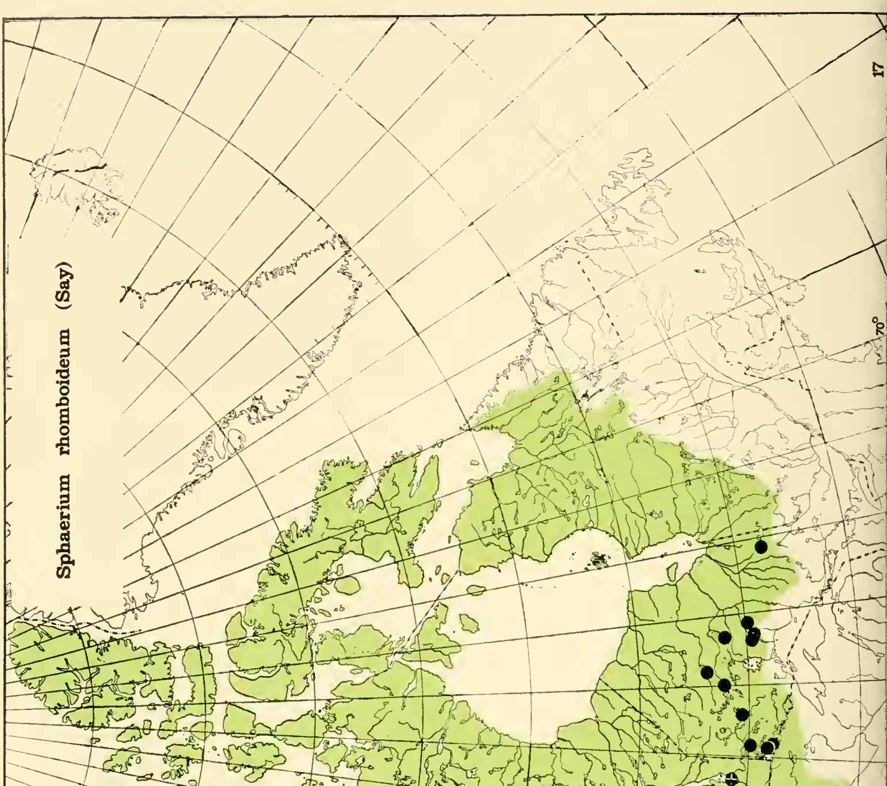
Description: " Shell moderately large, much inflated, walls thin; beaks central, low and broad, but begin rather narrow; striae fine and regular (very fine on beaks); periostracum glossy; dorsal margin gently curved and moderately long; ventral margin almost straight and very long; anterior end somewhat pointed and rounded joining dorsal and ventral margins without an angle; posterior end somewhat truncate, joining dorsal margin with a slight angle, and ventral margin with a greater angle. These angles vary in different specimens. The ends tend to taper outward as they descend, and the greatest length of the shell is rather low. Hinge long, gently but not evenly curved, bending between the cardinals and the anterior laterals; hinge-plate long, of even width...Most specimens of this species have definite bands of color, the latest growth being lighter than the older part of the shell. The nepionic young are somewhat square in outline with the anterior end not so vertical as the posterior." (Herrington, 1962: 25).

Measurements (in mm) :

Spec. No.	L	H	H/L	W	W/L
Sturgeon Lake, Sask.					
1	9·6	8·1	0·84	5·8	0·60
5	9·0	7·3	0·81	5·2	0·58
9	8·5	7·2	0·85	5·0	0·59
13	7·7	6·5	0·84	4·1	0·53
Willow Bend Creek, 9 mi W of Portage la Prairie, Man.					
1	9·2	7·3	0·79	5·2	0·57
5	8·3	7·1	0·86	4·5	0·54
9	7·8	6·5	0·83	4·1	0·53
13	6·9	6·0	0·87	3·3	0·48
Small lake 3 mi N of Geraldton, Ont.					
1	13·7	11·5	0·84	8·6	0·62
5	12·2	9·7	0·80	7·1	0·58
9	10·5	8·6	0·81	6·1	0·58
13	9·1	7·8	0·86	4·7	0·52

Records:

Ontario. Lillabelle Lake, 4 mi and 5 mi N of Cochrane (2 localities). Lydia Lake, 23 mi E of Longlac. Unnamed small lake 16 mi NW of Nakina. Kenogamisis Lake, 7 mi SE of Geraldton (all this survey). Attawapiskat Lake (52°18′N, 87°54′W) (1962, Ont. Dept. Lands and Forests!). Lake St. Joseph (51°05′N, 90°35′W) (1905, W. McInnes!). Lac Seul (1919, F. W. Waugh!). Off Lake at outlet, 4 mi NE of Finland (this survey). " Between


Sphaerium rhomboideum (Say)
17
70°
100°
45°
45°

Saganagons and Othermans lakes" [near 48°15′N, 91°04′W] (Baker, 1939b: 90). One-Sided Lake [Caliper Lake], about 60 mi SE of Kenora, Old Woman Lake, 35 mi S of Kenora (both this survey).

Manitoba. Willow Bend Creek, 9 mi W of Portage la Prairie (this survey). Pine Creek and Lake Winnipeg (Dall, 1905: 136).

Saskatchewan. Whitesand River, 9 mi ESE of Sheho. Stream 4 mi N of La Ronge (both this survey). Sturgeon Lake (53°25′N, 106°06′W) (1955, D. S. Rawson!).

Alberta. Caché Lake, 2 mi W of Spedden (this survey).

Distribution: New Brunswick northwest to British Columbia and Alaska (?) south of tree-line; Maine to Pennsylvania and across the northern tier of states to Idaho.

Biology and Ecology: The 12 collections of *Sphaerium rhomboideum* made during this survey came from 3 large lakes, 4 small lakes, and 5 streams of various widths between 25 and 15 feet. Current was slow at 4 stream localities and moderate at one. Vegetation was thick or medium thick at all stations but one; there it was sparse. Bottom sediments were predominantly of mud except at 2 localities, at 1 it was of gravel and at the other of sand and gravel.

Herrington (1962: 25) gives eddies in creeks and rivers and sheltered places in small lakes, both with muddy bottoms, weeds, and algae, as the preferred habitat of this species. The above records corroborate this statement and extend it to include muddy parts of large lakes and (rarely) gravel bottoms of rivers, with or without sand. The records in Baker (1928b: 346) agree with those from this survey.

Adult specimens were examined for enclosed juveniles, with the following results:

Adult Length, mm	No. of Young	Length of Young, mm
Stream 4 mi N of La Ronge, Sask. (July 28, 1962).		
12·5	9	4·1(1), 4·0(1), 3·6(1), 3·5(3), 1·4(3)
Willow Bend Creek, 9 mi W of Portage la Prairie, Man. (July 9, 1965).		
11·0	11	3·9(1), 3·6(1), 3·4(2), 3·3(1), 2·0(1), 1·8(2), 1·5(2), 0·8(1)
Lillabelle Lake, 4 mi N of Cochrane, Ont. (July 31, 1960)		
11·1	3	3·0(1), 2·4(2)
Small stream 3 mi N of Geraldton, Ont. (July 20, 1961).		
8·9	2	1·0(2)

Sphaerium (*Sphaerium*) *simile* (Say)
Plate 10, Figs. 6, 7; Map 18.

Cyclas similis Say, 1816: *Nicholson's Encyclopedia.* 1st Amer. ed., pl. 1, fig. 9 (Binney reprint, 1858: 54). Type locality: "in the river Delaware." For discussion of the validity of this name see Baker (1964: 45, and included references) and Herrington (1965: 44).

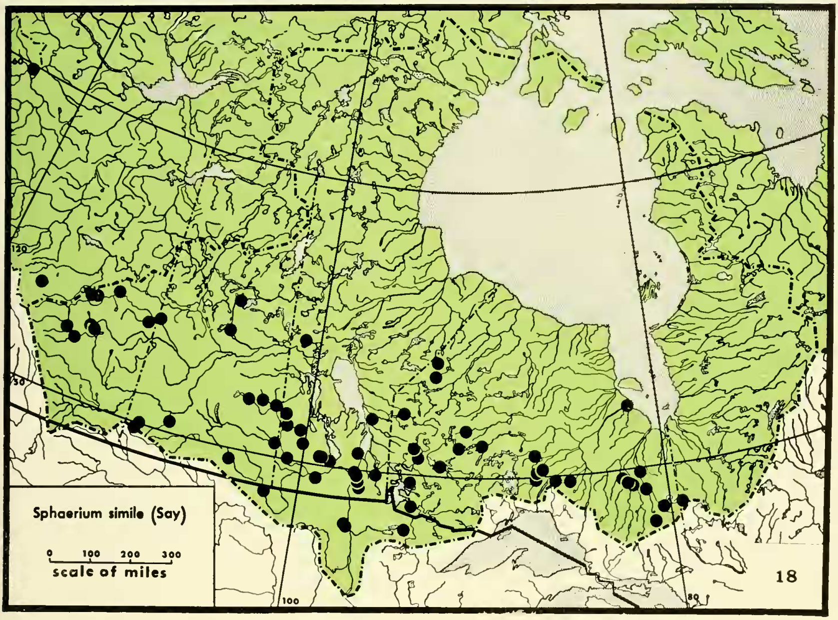
Cyclas sulcata Lamarck, 1818: *Hist. natr. Animaux sans Vertèbres.* Ed. 1, *5:* 560 (1st page having this number). Type locality: "lac Georges, Amérique septentrionale [Lake George, New York]."

Diagnosis: Shell up to about 1 inch long; moderately thick and strong; long-ovate; with subcentral umbones; heavy, evenly-spaced striae; bluish interior; and (in many specimens) with prominent concentric lighter and darker bands.

Description: "Shell large, heavy, long in outline; beaks low, subcentral; striae heavy, more widely spaced around beaks than farther out, and of fairly uniform height; periostracum a dull gloss; dorsal margin long, slightly rounded; ventral margin long, a little more openly rounded; anterior end slightly rounded, steep but not vertical slope [*sic* ! vertically sloped], joins dorsal margin with or without an angle and ventral margin low with a much-rounded angle; anterior and posterior ends similar; hinge long, very openly curved, narrowing somewhat and with a slight dip between cardinals and anterior cusps; hinge-plate rather long, moderately narrow; laterals short to medium in length;...." (Herrington, 1962: 28).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Pond 10 mi S of Cochrane, Ont.					
1	22·5	16·5	0·73	12·0	0·53
5	21·9	15·8	0·72	11·6	0·53
9	21·0	15·4	0·73	10·4	0·50
13	20·3	15·1	0·74	10·2	0·50
Minnedosa River, 11 mi NNE of Elphinstone, Man.					
1	19·5	14·6	0·75	10·6	0·54
5	18·6	14·1	0·76	9·7	0·52
9	17·4	12·8	0·74	8·9	0·51
13	15·7	11·5	0·73	8·2	0·52
Blindman River, 5 mi N of Red Deer, Alta.					
1	20·1	15·8	0·79	11·0	0·55
5	18·2	13·6	0·75	10·6	0·58
9	17·1	13·0	0·76	9·8	0·58
13	16·3	12·7	0·78	9·3	0·57



Records:

More than 85 lots are available from the collection area, so only marginal records are cited below.

Quebec. Lake Abitibi at Baie La Sarre, 3 mi WNW of Palmarolle (this survey).

Ontario. St. Ann's Lake, Sinclair Island, Fort Albany. Unnamed lake, headwaters of Sachigo River (53°37′N, 92°40′W), Stout Lake, at outlet (52°08′N, 94°44′W) (all this survey).

North Dakota. Mouse River [Souris River], 15 mi WNW of Mohall (this survey).

Manitoba. Red Sucker Lake, west end (54°10′N, 93°57′W) (Hayes River system) (this survey).

Saskatchewan. Montreal Lake, 16 mi N of Waskesiu Lake. Lac la Ronge, La Ronge (both Churchill River system) (this survey).

Alberta. Blindman River, 5 mi N of Red Deer. White Earth Creek 4 mi NE of Smoky Lake. Sturgeon River, 3 mi N of Villeneuve (all this survey). Obed Lake, near Hargwen (1925 L. S. Russell!).

British Columbia. Crooked Lake (59°52′N, 126°24′W) (1961, P. M. Youngman!).

Distribution: New Brunswick to the vicinity of James Bay and westward to northern and central British Columbia (NMC records), also south to Virginia, Iowa, and Wyoming (Herrington, 1962: 29).

Biology and Ecology: The 55 lots of *Sphaerium simile* collected during this survey came from all sorts of permanent-water habitats, i.e., 16 from large lakes, 6 from small lakes, 2 from permanent ponds, 4 from rivers over 100 feet wide, 12 from rivers 50 to 100 feet wide, 11 from rivers 25 to 50 feet wide, 3 from streams 10 to 25 feet wide, and 1 from a stream under 10 feet in width. Current was moderate to slow at most lotic sites. Submersed vegetation was present at all sites and bottom deposits were of all types, with mud or sand or both the most frequent.

Herrington (1962: 29) gives the habitat of this species as: " Small lakes, also eddies in rivers and creeks. It has a preference for soft sand with vegetation; [it is] never found in swamps or ponds. " The 2 ponds reported as sites for *Sphaerium simile* are each estimated as about 4 to 5 acres in area and would probably qualify as small lakes using Herrington's criteria.

The anatomy of *Sphaerium simile* has been described by Drew (1896) and Gilmore (1917).

The siphons of *Sphaerium simile* (from Carp River, Carp, Ont.) are short, triangular, joined at the base, and yellow. The foot is long, wide, subcylindrical when fully extended, white, and issues from the shell margin anterior to the mid-ventral position. The animal is quite active and when specimens are replaced in water a few hours after having been collected they resume activity within a few minutes.

Adult specimens were examined for enclosed young with the following results:

Adult Length, mm	No. of Young	Length of Young, mm
Medcalfe Lake, 63 mi N of Savant Lake, Ont. (Aug. 8, 1961).		
17·9	2	3·1, 2·5
15·5	2	3·6, 2·5
14·5	2	4·4(2)
Minnedosa River, 11 mi NNE of Elphinstone, Man. (July 10, 1965).		
19·6	4	7·4, 6·7, 4·8, 2·7
17·9	4	7·0, 6·3, 3·1, 2·7
Assiniboine River, 3 mi NE of Amsterdam, Sask. (July 28, 1965).		
17·7	5	1·6(2), 0·8(3)
Swift Current Creek, 3 mi N of Waldeck, Sask. (June 10, 1965).		
15·2	17	5·5, 5·0, 2·8, 2·4 2·2, 1·7(4) 0·9 or less (8)

Gilmore (1917: 26) presented evidence based on what appear to be annual growth rests that *Sphaerium simile* may live for at least 8 years.

Sphaerium (*Sphaerium*) *striatinum* (Lamarck)
Plate 16, Fig. 1; Map 19.

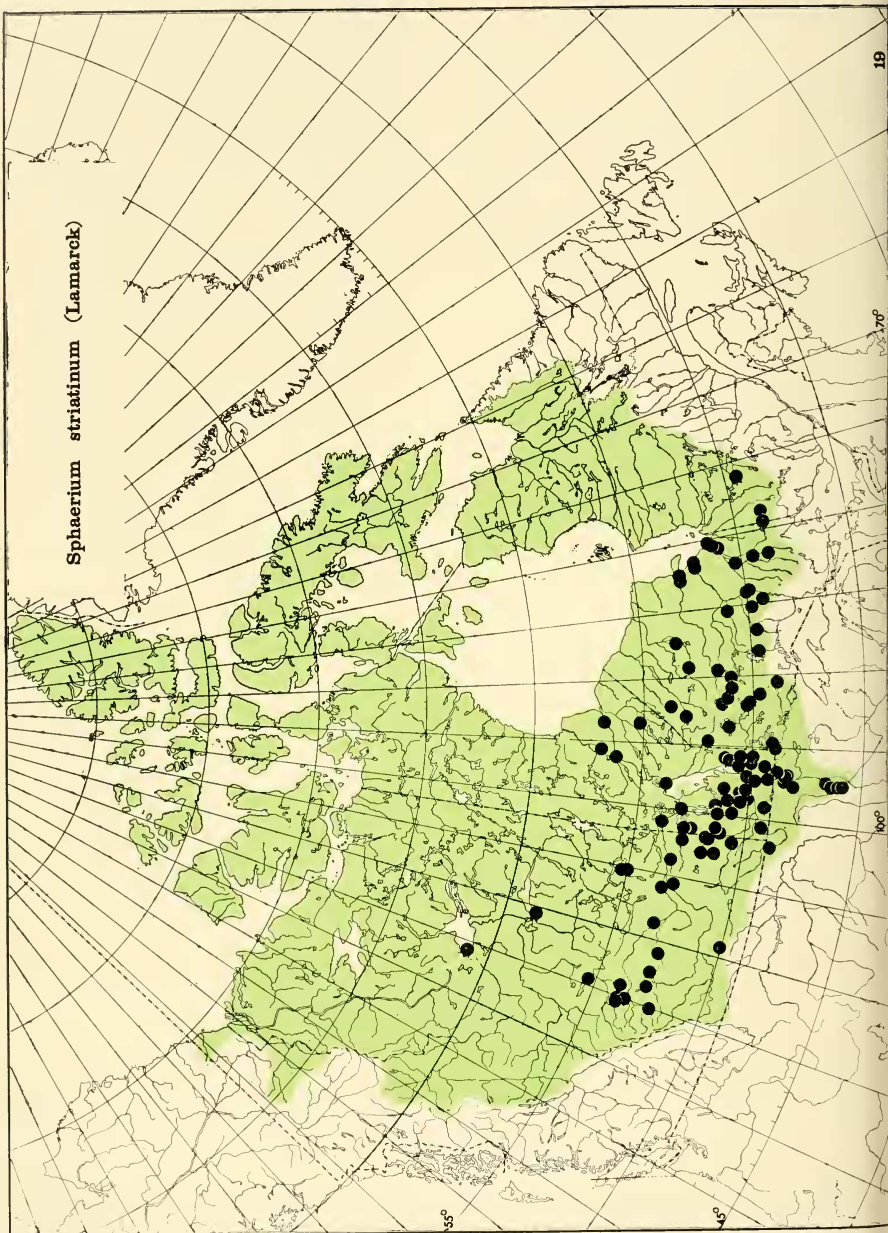
Cyclas striatina Lamarck, 1818: *Hist. Natr. Animaux sans Vertèbres.* Ed. 1, *5*: 560 (1st page thus numbered). Type locality: "lac Georges, Amérique septentrionale [Lake George, New York]."
Cyclas triangularis Say, 1829: *N. Harmony Dissem. useful Knowl.*, *2*: 356. (Binney reprint, 1858: 138). Type locality: "Mexico."
Cyclas solidula Prime, 1851: *Proc. Boston Soc. natr. Hist.*, *4*: 158. Type locality: "Ohio."

Diagnosis: Shell up to about 3/5 inch long, variable, moderately thick and strong; subovate, with umbones slightly anterior of centre, striae weak to strong and unevenly-spaced, interior bluish or whitish, exterior in many specimens with well-marked growth rests but without prominent alternating dark and light concentric bands.

Description: "Shell medium to large, moderately inflated, shell wall moderately thin to fairly thick; beaks somewhat toward anterior end, low to prominent; striae irregular; some specimens heavily striated over whole shell, some have heavy striae on beaks, but they almost fade out toward outer part of shell; in some, striae are faint on beaks, but become heavier farther out; in other sets, striae can hardly be seen; periostracum dull (the lake form sometimes attains some gloss); dorsal margin of medium length, roundly and fairly evenly curved; ventral margin long and more openly curved; anterior end roundly curved, joining dorsal margin without an angle and ventral margin with or without a rounded angle; posterior end usually a slope joining margins with or without an angle; hinge fairly long, considerably and unevenly curved,..." (Herrington, 1962: 27).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Frog Rapids, Abram Lake, Sioux Lookout, Ont.					
1	11·5	10·3	0·90	7·7	0·67
5	11·0	9·4	0·85	7·4	0·67
9	10·8	9·8	0·91	7·4	0·69
13	10·3	8·9	0·86	7·0	0·68
Assiniboine River, western edge of Winnipeg, Man.					
1	13·2	11·3	0·86	7·9	0·60
5	11·2	9·5	0·85	6·9	0·62
9	10·6	9·0	0·85	6·8	0·64
13	10·0	8·5	0·85	6·4	0·64
Sturgeon River, 3 mi N of Villeneuve, Alta.					
1	11·8	9·1	0·77	6·6	0·56
5	11·2	8·7	0·78	6·1	0·54
9	10·3	8·0	0·78	5·6	0·54
13	9·5	7·4	0·78	5·1	0·54


Sphaerium striatinum (Lamarck)
19
70°
100°
55°
45°

Records:

Since nearly 150 lots of *Sphaerium striatinum* are available from the research area, only marginal records are listed.

Quebec. Small river 9 mi NE of Demaraisville. Lake Abitibi at Baie la Sarre, 3 mi WNW of Palmarolle. Macamic Lake, north end, 11 mi E of La Sarre (all this survey).

Ontario. Moose River, Moose Factory. Albany River, near Fort Albany (5 localities). Attawapiskat River, near Attawapiskat (2 localities) (all this survey). Bashka Rapids, Winisk River (55°17′N, 85°05′W) (1903, W. McInnes!). Winisk Lake (52°55′N, 87°22′W). Sachigo Lake (53°49′N, 92°08′W). Sandy Lake (53°02′N, 93°00′W) (all 1964, Ont. Dept. Lands and Forests!). Stout Lake, at outlet (52°08′N, 94°44′W) (this survey).

Manitoba. Knee Lake (55°03′N, 94°40′W) (1905, O. O'Sullivan!). Recluse Lake, Little Churchill River (56°55′N, 95°45′W) (this survey).

Saskatchewan. Lac la Ronge, from whitefish stomachs (1954, Univ. Sask.!).

Alberta. Lake Athabasca, west end (Herrington, 1950: 28).

Northwest Territories. Great Slave Lake, west end (1919, R. A. Brooke!). Great Slave Lake, 2–3 m depth (Herrington, 1950: 27). Empty, bleached shells have also been seen from the mouth of Hay River, from Mills Lake, and from Fort Norman but their ages are unknown.

Distribution: New Brunswick to the head of James Bay and northwest to Great Slave Lake and the Upper Yukon River (unnamed lake at 68°03′N, 139°55′W, NMC record) south throughout the United States at least to Vera Cruz, Mexico; also Panama (this survey and Herrington, 1962: 28).

Biology and Ecology: Seventy-six lots of *Sphaerium striatinum* were collected during this survey from the following habitats: 10 are from large lakes, 1 from a small lake, 34 from rivers over 100 feet wide, 16 from rivers 50 to 100 feet wide, 10 from rivers 25 to 50 feet wide, 2 from streams 10 to 25 feet wide and 3 from streams less than 10 feet wide. Current was present at all lotic stations and of various velocities from rapid to slow. Vegetation was present at all but was sparse at most, and bottom deposits were of all types. Mud was the most frequent but rocks, gravel, and sand substrates were common.

According to Herrington (1962: 28) this species inhabits "creeks, rivers, [and] large and small lakes." It does not occur in "ponds, swamps, or anywhere in stagnant water." Coarse sediments are said to be suitable and fine, soft mud unsuitable.

Adult specimens of this species were examined for enclosed young, with the following results:

Adult Length, mm	No. of Young	Length of Young, mm
Qu'Appelle River, 4½ mi W of Welby, Sask., (July 12, 1965).		
14·0	2	2·9, 1·2
13·6	5	4·9, 2·8, 2·3, 1·3, 1·1
13·6	4	5·9, 3·4, 2·2, 1·4
Turtle River, Edam, Sask., (July 14, 1965).		
14·3	6	4·5, 4·2, 3·7, 2·6, 2·4(2)

Adult Length, mm	No. of Young	Length of Young, mm
Whitemud River, Gladstone, Man., (July 12, 1962).		
12·3	3	4·5, 2·1, 0·9
Souris River, ½ mi S of Souris, Man., (Aug. 6, 1962).		
11·7	3	4·0, 2·1, 1·5
Rat River, 1½ mi S of La Rochelle, Man., (Aug. 9, 1964).		
10·7	3	2·6, 1·7, 1·3
Seine River, Grande Pointe, Man., (Aug. 9, 1964).		
12·3	9	all about 0·7
11·6	8	4·2, 3·5, 1·9, 1·7, 1·0(4)

Details of the anatomy and life history of *Sphaerium striatinum* have been described by Monk (1928, as *S. notatum*), Woods (1931), and Foster (1932, as *S. solidulum*).

Remarks: This species is quite variable, lake specimens being often relatively high and river specimens relatively long, according to Herrington (1962: 27). Inspection of available material supports this generalization (e.g., see " Measurements ") although all intergrades also occur. The data in Herrington (loc. cit.) and Baker (1928b : 331, etc.) imply that valid subspecies may exist but probably not in the region covered by this survey.

Subgenus **Herringtonium** (new subgenus)

Type species: *Cyclas occidentalis* Prime 1856, by original designation.

Sphaerium (*Herringtonium*) *occidentale* (Prime) exhibits characters which are similar to those in *Sphaerium* (*s. str.*) but different from those in the subgenus *Musculium* Link 1807, characters which are similar to those in *Musculium* but different from those in *Sphaerium* (*s. str.*), and other characters not seen in either of those subgenera. It is similar to *Sphaerium* (*s. str.*) (and different from *Musculium*) in general shell shape, in lacking calyculate umbones, and in that relatively few young are held within an adult. It is similar to *Musculium* (and different from *Sphaerium* (*s.str.*)) in that its shell is relatively more fragile and in that the young of a single brood are all the same size. It also differs from native North American *Sphaerium* (*s. str.*)) in the possession of fine striae. It is unique, however, in the possession of a low radial ridge on the central inner surface of each valve and in that its habitat is exclusively in vernal water bodies.

The habit of bearing only a few young all of the same size has been observed in Canadian specimens. This is probably adaptive and related to habitat. Presum-

ably, young must be released at approximately the same time during an optimum period when the habitat contains water. Since fish predators are absent in vernal habitats small numbers of young may also be adaptive for population control and survival.

Sphaerium occidentale appears not to be closely related to any other species. Recognition of the species as a monotypic subgenus also enables *Sphaerium* and *Musculium* to be separated more completely by mutually exclusive characters.

This new taxon is named in honour of Rev. H. B. Herrington who for over 30 years has been the foremost student of the Sphaeriidae in North America. By a coincidence and entirely independently both W. H. Heard and I had recently decided to propose a new subgenus of *Sphaerium* named for Rev. Herrington. We had not intended to designate the same type species, however, and Dr. Heard requested me to proceed with publication.

Sphaerium (*Herringtonium*) *occidentale* (Prime)

Plate 16, Fig. 4; Map 20.

Cyclas ovalis Prime, 1853: *Proc. Boston Soc. natr. Hist.*, *4*: 276. Type locality: "Oswego and Greenwich, New York [and] Columbus, Ohio."

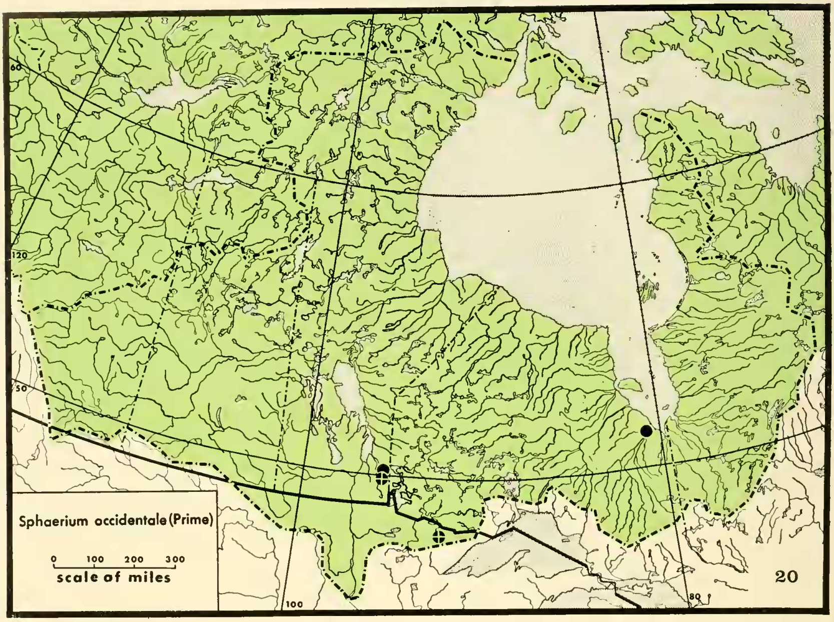
Cyclas occidentalis Prime (*in* Lewis), 1856: *Proc. Boston Soc. natr. Hist.*, *6*: 2. New name for *Cyclas ovalis* Prime, 1853 *non* Ferrusac, 1807.

Diagnosis: Shell up to about $\frac{1}{3}$ inch long, rather fragile, evenly ovate, and with slightly elevated, centrally located umbones, with fine concentric striae which are even finer on the umbones, and with a central radial ridge inside each valve.

Description: "Shell small, rounded, a little longer than high, moderately inflated, "rest periods" prominent, walls of shell thin, about as high in front of beaks as behind; beaks moderately narrow and not very high, about central; striae fairly fine, becoming finer as beaks are approached; periostracum dull or having a dull gloss;. . .hinge very long (almost full length of shell); hinge-plate long, slim (slightly heavier in ditch and pond forms), very gently, evenly curved and of uniform width; laterals fairly slim, those of the left valve and the inner ones of the right valve moderately long; cusps of left valve and inner cusps of right valve sharp or only slightly blunted on top. . . There is a ridge on the inside of the shell about midway between the ends, and reaching from near the beaks to the ventral edge of the shell. The dorsal margin of the nepionic young is almost straight, and the ends are well rounded." (Herrington, 1962: 22).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Otter Falls, Whiteshell Provincial Park, Man.					
1	3·8	3·0	0·79	1·7	0·45
Moose Factory, Ont.					
1	7·3	6·2	0·85	3·9	0·53
2	6·5	5·7	0·88	3·5	0·53



Records:

Ontario. Swamp north of Hudson Bay Co. post, Moose Factory (2 adults) (July 28, 1950, J. L. Chamberlin!).

Manitoba. Otter Falls, Whiteshell Provincial Park (1 juvenile) (July 26, 1964, F. R. & J. C. Cook!). "Mile 69, G.W.W.D. Ry., near the settlement known as Birch River.* Shallow railway ditch." (Mozley 1926a: 123).

Minnesota. Swampy brook behind beach, Daisy Bay, Vermilion Lake (Baker, 1929: 96).

Distribution: New Brunswick to southeastern Manitoba, west to Washington, and south to Georgia in the east and to Utah and Colorado in the west. The records are widely and unevenly distributed. In the Canadian Interior Basin it is at present recorded only from northeastern Ontario, southeastern Manitoba, and northern Minnesota.

Biology and Ecology: "Stillwaters of swamps, ditches, and ponds; among grass and leaves. This species has a preference for, or requires, a habitat that dries up for part of the year" (Herrington, 1962: 22). The habitats reported above agree with this. The species is sometimes found living among damp leaves entirely out of water and is probably more amphibious than any other North American bivalved mollusc.

Herrington (1948a: 74) has shown that *Sphaerium occidentale* lives for at least 2 to 3 years and is often extremely abundant where it occurs. He collected

* Not the present village of Birch River (52°23′N, 101°06′W) but near Reynolds, Man. at 49°39′N 95°50′W.

2,536 complete specimens (both valves) at 1 time within a circle of 6 feet diameter from a swamp 4 mi NNW of Newburgh, Ontario in 1944.

Baker (1928b: 348) has briefly described the soft anatomy as similar to *Sphaerium simile*, with gills wide and united above, labial palps long and narrow, and foot large, transparent, and usually protruded from the centre of the base of the shell.

Six specimens from Canada and Montana were examined for included young, with the following results:

Adult Length, mm	No. of Young	Length of Young, mm
Moose Factory, Ont. (July 28, 1950).		
6·5	2	1·9 (2)
7·3	3	2·0 (3)
Swamp 4 mi N of Newburgh, Ont. (June 29, 1964).		
6·4	3	less than 0·6 (3)
6·6	5	less than 0·6 (5)
Pond 2 mi S of Thomasburgh, Ont. (Aug. 25, 1939).		
6·5	2	1·9 (2)
Marsh, Glacier National Park, Mont. (June 24, 1966).		
7·5	4	1·7 (4)

Remarks: The apparent isolation of living *Sphaerium occidentale* at Moose Factory, over 300 miles from the nearest recorded localities farther south (the upper peninsula of Michigan (Heard, 1962: 147)) is anomalous and similar to the distribution of *Armiger crista*. As mentioned elsewhere, the James Bay lowlands, in contrast to the surrounding Precambrian Shield, are rich in calcareous deposits. The occurrence of *S. occidentale* in that region may be indicative of a more continuous northern distribution about 4,000 to 6,000 years ago during the Hypsithermal Period. Additional collections of both species are needed to test this hypothesis, however.

Subgenus *Musculium* Link

Musculium Link 1807: *Beschr. Natr. Samml. Univ. Rostock*, *3*: 152. Type species: *Tellina lacustris* Müller, by subsequent designation (Mörch, 1862: 228).

Adult specimens from about 6 to 12 mm long, shell walls thin to moderately thick, striae fine, shell truncate posteriorly and without a low, radiating, internal rib. Umbones calyculate, i.e., " capped ". Embryonic young inside a single adult number up to about 34 and tend to be either all of the same size or grouped into a few (up to 4) broods of individuals, which are all of the same size within each brood but different in size from the individuals

of other broods. Habitat: in perennial and vernal water bodies.

Four species of this subgenus occur in North America and all extend northward into the area of the present survey. Geologic range: Miocene to Recent.

Sphaerium (*Musculium*) *lacustre* (Müller)
Plate 16, Fig. 9; Map 21.

Tellina lacustris Müller, 1774: *Vermium terrestrum et fluviatilium* (etc.), *2*: 204. Type locality not specified.
Cyclas ryckholti Normand, 1844: *Notice des cyclades.* p 7. Type locality: Europe.
Cyclas jayensis Prime, 1852: Descriptions of *Cycladidae. Proc. Boston Soc. natr. Hist.*, *4*: 157. Type locality: " Lake Superior."
Musculium winkleyi Sterki, 1909: Descriptions of two new species of *Musculium. Nautilus, 23*(5): 66. Type locality: " Old Orchard, Me."

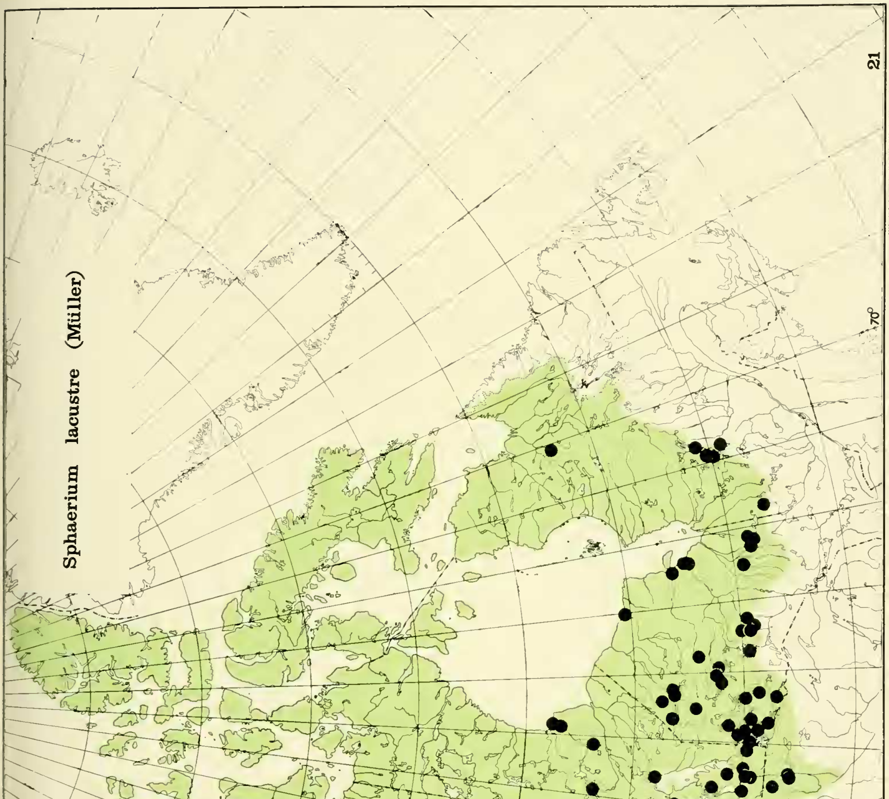
Diagnosis: Shell up to about ½ inch long, relatively fragile, trapezoidal to rhomboidal in shape, with prominent, projecting umbones, rounded dorsal margin and broadly-curved ventral margin.

Description: " Shell small to medium size, walls thin, little to considerably inflated, anterior end not so high as the posterior; beaks somewhat toward anterior end, swollen and full, varying in height, usually capped, but not always, caps vary from large to small; striae moderately fine to fine, uneven (surface not as smooth as in *Sphaerium partumeium*); periostracum a slightly dulled gloss...The ends are seldom parallel, but slope up toward the dorsal margin. Sometimes the posterior end has a much longer slope than the anterior, in which case the lower part extends farther out. Hinge very long, slightly to considerably curved, usually with a bend behind the cardinals; hinge-plate fairly long and very narrow, sometimes almost absent and then the laterals seem to be attached to the walls and the cardinals are partly suspended over space; laterals slim but distinct...The hinge-plate is so narrow that the cardinals are delicate and vary greatly in shape and direction. " (Herrington, 1962: 19).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Whitesand River, 7 mi E of Sheho, Sask.					
1	7·2	6·6	0·92	4·4	0·66
5	6·8	6·4	0·94	4·0	0·58
9	6·6	6·0	0·90	3·8	0·57
13	5·8	5·5	0·94	3·6	0·62
Willow Bend Creek, 9 mi W of Portage la Prairie, Man.					
1	8·6	7·2	0·84	5·4	0·63
5	7·5	6·8	0·90	5·1	0·68
9	6·9	6·2	0·89	4·4	0·64
13	6·5	5·9	0·90	4·2	0·65
Oxbow lake near Devil's Gut, Albany River estuary, Ont.					
1	4·3	4·2	0·97	2·8	0·65
5	3·6	3·2	0·89	2·1	0·58
9	3·4	2·8	0·82	1·9	0·56
13	3·1	2·5	0·81	1·6	0·52

Herrington (1962: 19) has recorded a specimen from Sunnyside, Lake Ontario, Toronto, Ont. which measures L, 14·0; H, 11·5; W, 8·2 mm. No specimens seen from the present research area exceed 11 mm in length.


Sphaerium lacustre (Müller)
21
70°
100°
55°
45°

Records:

Approximately 125 collections of this species are available from the research area. These are plotted on Map 21 and only marginal records are cited below.

Quebec. Lac Aigneau (57°10′N, 70°35′W) (1955, D. R. Oliver!). Rivière à la Perche, 48 mi NE of Chibougamau (this survey).

Ontario. Albany River estuary near Fort Albany (three localities). Attawapiskat River, 6 mi W and 20 mi W of Attawapiskat (two localities). Winisk River, 22 mi S of Winisk (all this survey).

Manitoba. Recluse Lake, Little Churchill River (56°55′N, 95°45′W). Goose Creek and mouth of Goose Creek, 7 mi S of Churchill (all this survey).

Northwest Territories. Lac la Martre (63°10′ 20″N, 117°20′W) (1959 Fish. Res. Bd.!).

British Columbia. Mile 550, Alaska Highway (near junction of Coal River and Liard River) (1962, S. D. MacDonald!).

Distribution: Throughout North America (except the southwestern United States) north to tree-line in Canada and Alaska. According to Heard (1963b: 106) it also occurs in Central and South America, Eurasia, Australia and the Hawaiian Islands.

Biology and Ecology: Of the 75 lots of *Sphaerium lacustre* collected during this survey, 14 are from large lakes, 10 from small lakes, 6 from permanent ponds, 1 from a roadside ditch (apparently vernal), 10 from rivers over 100 feet wide, 9 from rivers 50 to 100 feet wide, 15 from rivers 25 to 50 feet wide, and 10 from streams 10 to 25 feet wide. The predominant substrate was mud, although at 8 stations only sand was observed. Submersed vegetation occurred at all localities but in varying abundance. Current was slow at most lotic localities although in a few it was rapid, moderate, or imperceptible.

According to Herrington (1962: 20) this species occurs " most plentifully in small lakes and ponds, but also found in large lakes, rivers, and creeks. " " Form *ryckholti* " is reported from ponds and bog-ponds and " form *jayense* " from mud in large lakes.

Six specimens from the survey area were examined for included young, with the following results:

Adult Length, mm	No. of Young	Length of Young, mm
Stream 6 mi SW of Oak Bluff, Man. (June 7, 1965).		
5·6	0	—
7·5	1	1·0
Small stream 4 mi N of La Ronge, Sask. (July 28, 1962).		
6·9	15	0·9(10), 1·4 (5)
7·5	6	1·3 (6)
9½ mi S of Two Hills, Alta. (Aug. 6, 1965).		
8·2	28	0·9 (12), 1·4 (16)
7 mi E of Spruce Grove, Alta. (July 14, 1963).		
6·5	7	1·1(7)

Remarks: A trend toward decreasing maximum size with increasing latitude is apparent in this species. Specimens from northern peripheral populations reach maximum lengths of only 5 to 6 mm, or less.

Two distinct morphs exist in addition to " typical " *Sphaerium lacustre*, viz., "form" *ryckholti* and "form" *jayense*. The *ryckholti* morph is roughly tri-

angular, with high beaks, a curved hinge, a short dorsal margin and a long, gently curved ventral margin. The *jayense* morph is nearly rectangular with relatively straight dorsal and ventral margins.

Typical *Sphaerium lacustre* occurs throughout the whole research area south of the tree-line. The *ryckholti* morph has been found at 25 localities, all west of the lime-poor Precambrian Shield. The *jayense* morph has been found at only 2 localities (Hamilton Lake, Ont. and Attawapiskat River, Ont.), both on the Precambrian Shield. Heard (1962: 147) states that in Michigan *ryckholti* does not occur south of the Grand-Saginaw River Valley and *jayense* does not occur north of it. That distribution does not correlate with the occurrence of limestone, which is abundant in both areas.

Clearly geological and geographical relationships exist with respect to the distribution of these morphs and the nature of these relationships needs to be more thoroughly studied.

Sphaerium (*Musculium*) *partumeium* (Say)
Plate 16, Fig. 6; Map 22.

Cyclas partumeia Say, 1822: *J. Acad. natr. Sci. Philad.*, *2*: 380. Type locality: "a pond near Germantown [Pennsylvania]."

Cyclas truncata Linsley (*in* Gould), 1848: *Amer. J. Sci.*, new ser. *6*: 324, fig. 3. Type locality: "Connecticut."

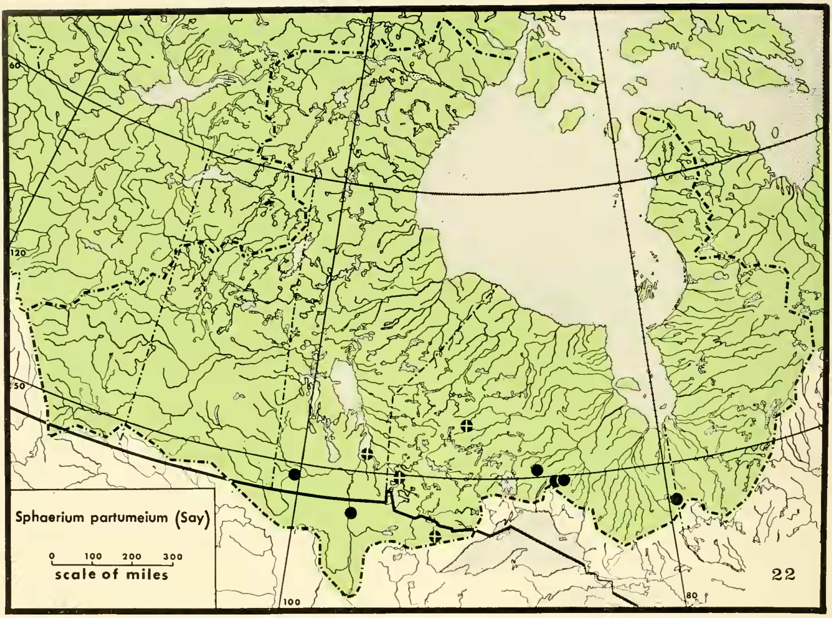
Diagnosis: Shell up to about ½ inch long, fragile, with fine striae, truncated posteriorly, and with umbones located centrally or anterior of centre.

Description: "Shell rather small to medium size, somewhat short in outline, walls thin; beaks about central or slightly anterior, low and but little swollen; striae fine and evenly spaced; periostracum glossy and smooth; dorsal margin almost straight and about as long as ventral margin; ventral margin well curved; anterior end usually well rounded, but sometimes slightly truncate, joining the dorsal margin with an angle and the ventral margin without an angle (except when slightly truncate; then it has a very slight angle); posterior end truncate, slightly rounded, vertical (i.e., at right angles to the dorsal margin, but at times the end is less steep and the lower part extends out somewhat), joining the dorsal margin with a sharp angle and the ventral margin with a less sharp one; hinge slightly rounded, long, same length as dorsal margin; hinge-plate rather long and very narrow (sometimes causing laterals to appear to be clinging to walls of shell)..." (Herrington, 1962: 23).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Taylor's Bush, Brittania, near Ottawa, Ont.					
1	7·3	6·3	0·86	4·1	0·56
5	7·1	6·2	0·87	3·8	0·53
9	6·3	5·6	0·88	3·6	0·57
13	5·8	5·1	0·88	3·2	0·55
Plum Creek, 9 mi W of Souris, Man.					
1	5·8	5·0	0·86	3·2	0·55

The largest specimen reported by Herrington (1962: 23) is from Parson's Slough, Trinity River, Texas and measures L, 13·5; H, 11·5; W, 9·0 mm.



Records:

Quebec. Lake Abitibi at Baie la Sarre, 3 mi WNW of Palmarole (this survey).

Ontario. Hamilton Lake [probably 51°51′N, 90°28′W; there are five Hamilton Lakes]. Skunk Lake, near Minaki (both Mozley, 1938: 119). Klotz Lake, 30 mi E of Longlac (dredged in 15 feet of water) Murky Creek, 27 mi N of Geraldton (both this survey).

Manitoba. Marsh bordering Lake Winnipeg, near Victoria Beach (Mozley, 1938: 119). Plum Creek, 2 mi N of a point 9 mi W of Souris (this survey).

Minnesota. Swamp behind beach, Birch Point, Big Bay, Vermilion Lake (Baker, 1929: 96).

Saskatchewan. "Saskatchewan" (Herrington, 1962: 24).

Distribution: Throughout the United States (except unrecorded from the extreme southwest) and in southern Canada from New Brunswick to Saskatchewan (Herrington, 1962: 24). The Lake Abitibi record (above) considerably extends the known range toward the northeast.

Biology and Ecology: The 4 habitats in which this species occurred are 2 large lakes and 2 slow-moving rivers, 1 about 100 feet wide and 1 about 20 feet wide. In all localities the substrate was of mud and vegetation was of medium abundance or sparse.

According to Herrington (1962: 24) *Sphaerium partumeium* occurs in "ponds, swamps, small lakes, and slow-moving streams. It has a preference for a muddy bottom, and is common." The above records partly confirm and extend this assessment to include muddy parts of large lakes. Elsewhere I have also found it in vernal ponds.

Baker (1928b: 355) briefly mentions the soft parts as generally whitish or with a shade of pinkish and with pink siphons. Thomas (1959: 131) reared

Sphaerium partumeium in the laboratory through 6 generations without cross-fertilization. The number of offspring produced by single individuals varied from 2 to 30 with a mean of about 10.

All specimens from the present research area were empty shells. Other specimens were examined for juveniles, however, with the following results.

Adult Length, mm	No. of Young	Length of Young, mm
Vernal pond, Newton, Mass.		
9·3	4	2·0, 1·9(3)
8·9	6	all 1·2
Lagoon, Bay of Quinte, Adolphustown, Ont.		
7·2	5	all 1·4

Sphaerium (*Musculium*) *securis* (Prime)
Plate 16, Fig. 8; Map 23.

Cyclas securis Prime, 1851: *Proc. Boston Soc. natr. Hist.*, *4*: 160. Type locality: " Fresh Pond [Cambridge Mass.] and in the Cambridge Meadows."

Cyclas sphaerica Anthony (*in* Prime), 1853: *Proc. Boston. Soc. natr. Hist.*, *4*: 275. Type locality: " Loraine County, O [hio]."

Diagnosis: Shell up to about ¼ inch long, fragile, with moderately coarse striae, truncated posteriorly, and with umbones centrally located.

Description: " Shell small, considerably inflated, much higher at posterior than at anterior end; walls fairly light; beaks sub-central, of moderate height and somewhat swollen (they do not readily blend into the shell, but frequently form a faint ridge extending across the shell toward the lower part of the posterior end; a slighter ridge is also sometimes discernible at the anterior end); striae fairly coarse to moderately fine, distinct and evenly spaced; periostracum dull, sometimes glossy...The dorsal margin is almost straight to slightly curved, fairly long; ventral margin a little longer than dorsal, well curved, and swinging high at anterior end, resulting in a greater disparity between the height of the anterior and posterior ends, in this species, than in any other *Sphaerium*; anterior end well rounded, sometimes with a slight slope, and joining the ventral margin without an angle, but frequently having an angle where it joins the dorsal margin; posterior end truncate, at right angles to dorsal margin, but sometimes extending out a little (then not quite vertical), joining dorsal margin with a fairly distinct, rounded angle, and ventral margin with a less distinct angle; hinge almost full length of shell, gently but not evenly curved..." (Herrington, 1962: 26).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Stream 4 mi N of La Ronge, Sask.					
1	5·8	5·2	0·90	3·4	0·59
5	5·3	4·5	0·85	2·9	0·55
9	5·0	4·3	0·86	2·8	0·56
13	4·1	3·5	0·85	2·2	0·54
Chadwick Lake, 16 mi E of Kenora, Ont.					
1	5·5	5·0	0·91	3·3	0·60
5	5·0	4·4	0·88	2·8	0·56
9	4·9	4·5	0·92	2·9	0·59
13	4·8	4·1	0·85	2·6	0·54
St. Ann's Lake, Sinclair Island, near Fort Albany, Ont.					
1	4·0	3·3	0·83	2·2	0·55
5	3·7	3·1	0·84	2·2	0·59
9	3·2	2·7	0·84	2·0	0·62
13	2·9	2·3	0·79	1·8	0·62

Records:

Quebec. Small river 9 mi NE of Demaraisville (this survey).

Ontario. Pools on bank of Albany River, Fort Albany. St. Ann's Lake, near Fort Albany. Yellow Creek, near Fort Albany. Klotz Lake, 30 mi E of Longlac. Unnamed small lake 3 mi N of Geraldton. Bamaji Lake, at cove on island (51°10′N, 91°25′W) (all this survey) Fitchie Lake (50°37′N, 90°32′W) (Mozley, 1938: 120). Nugget Creek, 12 mi E of Dryden. Pelican Lake, Sioux Lookout. Frog Rapids, Abram Lake, Sioux Lookout. Lake 12 mi S of Sioux Narrows. Chadwick Lake, 16 mi E of Kenora. Old Woman Lake, 35 mi S of Kenora (all this survey). "Alice Lake," between Minaki and Wade (Mozley, 1938: 120). Stout Lake, at outlet (52°08′N, 94°44′W) (this survey).

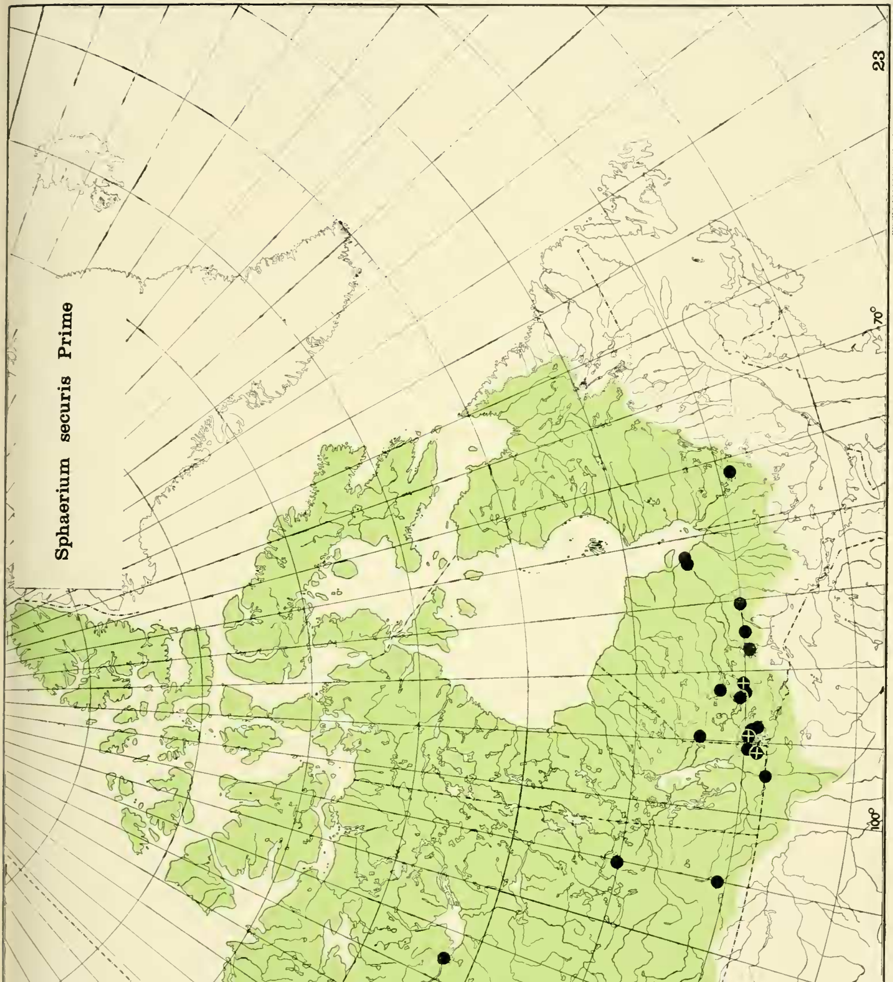
Manitoba. Brereton Lake (Mozley, 1938: 120). Pond near Falcon Lake. Marais River, 9 mi NW of Emerson. Stream 6 mi SW of Oak Bluff (all this survey).

Saskatchewan. Creek 4 mi E of Pense. Stream 4 mi N of La Ronge (both this survey).

Alberta. Inlet of Horn Lake, 10 mi SW of Whitecourt, Alta. (this survey).

Northwest Territories. "Little Lake" [Mills Lake] (61°30′N, 118°20′W) (1917, E. M. Kindle!).

Distribution: In Canada *Sphaerium securis* occurs from Newfoundland and Nova Scotia west to British Columbia and the southwestern part of the Northwest Territories (Mills Lake). In the United States it is recorded from most states except those in the southwest.


Sphaerium securis Prime
23
70°
100°
55°
45°

Biology and Ecology: The 20 survey localities for *Sphaerium securis* are as follows: 5 are large lakes, 5 are small lakes, 3 are permanent ponds, and 7 are slow-flowing rivers and streams from about 100 to 20 feet in width. Vegetation was thick to moderately thick at all stations and the predominant substrate was mud.

Herrington (1962: 26) gives the habitat as " Ponds, lakes and rivers. Frequently found in fine sand." Baker (1928b: 361-2) cites swales, lakes, pools and a river as sites for this species and gives the usual substrate as mud. Sand was noted at only 5 of the 19 survey stations and sand occurred without mud at only 1 (Frog Rapids, Abram Lake).

Specimens were examined for juveniles with the following results:

Adult Length, mm	No. of Young	Length of Young, mm
Pond near Falcon Lake, Man. (June 13, 1961).		
4·5	1	0·8
Chadwick Lake, 16 mi E of Kenora, Ont. (July 30, 1965).		
6·3	7	1·5(7)
5·2	7	1·4(2), 1·0(5)
Pelican Lake, Sioux Lookout, Ont. (Aug. 1, 1961).		
5·6	2	1·4(2)

Sphaerium (*Musculium*) *transversum* (Say)
Plate 16, Fig. 3; Map 24.

Cyclas transversa Say, 1829: *N. Harmony Dissem. useful Knowl.*, *2*: 356 (Binney reprint. 1858: 138). Type locality: " Kentucky."

Diagnosis: Shell up to slightly over ½ inch long, rather fragile, relatively elongate (height ¾ of length, or less). Habitat chiefly in rivers.

Description: " Shell quite large (but in some marginal localities rather small); long in outline; posterior end higher than anterior, walls thin; beaks nearer anterior end, the percentage with caps very small and then only weakly marked off; striae moderately fine, somewhat irregular; periostracum dull to slightly glossy; dorsal margin rather long, little curved, a jog at the beaks; ventral margin very gently curved, considerably longer than the dorsal; anterior end a steep slope with curvature of varying degrees or rounded,...posterior end being quite high, sloping outward with a somewhat rounded slope...hinge long, slightly and irregularly curved hinge-plate long, narrow, and forming a distinct jog behind cardinals; laterals distinct ..." (Herrington, 1962: 29).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Lake Abitibi, 3 mi WNW of Palmarolle, Que.					
1	9·5	6·9	0·73	4·1	0·43
5	8·2	6·0	0·73	3·8	0·46
9	7·8	5·9	0·76	4·0	0·51
13	5·2	3·9	0·75	2·5	0·48
Mouse River, 15 mi WNW of Mohall, N.D.					
1	12·7	9·0	0·71	6·4	0·54
5	11·2	8·2	0·73	5·5	0·49
9	10·8	8·3	0·77	5·7	0·53
13	9·4	6·6	0·70	4·5	0·48
Lake Winnipeg, 20 mi S of Gimli, Man.					
1	11·2	7·8	0·70	4·9	0·44
5	10·5	7·1	0·68	4·8	0·46
9	10·2	7·1	0·70	4·6	0·45
13	9·6	6·5	0·68	4·3	0·45

Records:

Quebec. Lac Dubuisson, 4 mi NW of Val d'Or. Lake Abitibi at Baie la Sarre, 3 mi WNW of Palmarolle (both this survey).

Ontario. Attawapiskat River, 6 mi W of Attawapiskat (this survey). Big Trout Lake (53°43′N, 90°00′W) and Finger Lake (53°09′N, 93°30′W) (1963 and 1961, both Ont. Dept. Lands and Forests!).

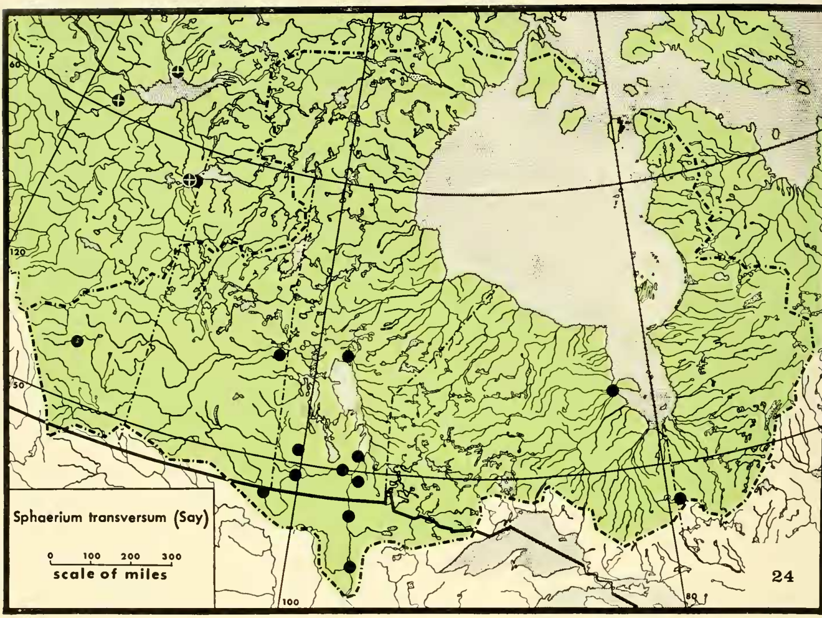
North Dakota. Red River, Abercrombie. Red River, 2 mi NE of Drayton. Mouse River [Souris River], Mouse River Park, 15 mi WNW of Mohall (all this survey).

Manitoba. Seine River, Grande Pointe, 12 mi SSE of Winnipeg. Assiniboine River, 12 mi NW of St. Francis Xavier. Souris River, 1/2 mi S of Souris. Minnedosa River, 10 mi NNW of Minnedosa (all this survey). Red River, Winnipeg (1890, collector?). Lake Winnipeg, 20 mi S of Gimli (this survey). Matlock, Lake Winnipeg (Mozley, 1938: 119). Playgreen Lake (1878, R. Bell!).

Saskatchewan. Carrot River, 50 mi SW of The Pas, Man. (this survey).

Alberta. "The Willows", Lake Athabasca (1945, D. S. Rawson!). Lake Athabasca, west end of lake, 1–5 m depth (Herrington, 1950: 28).

Northwest Territories. Great Slave Lake, Yellowknife Bay (Herrington, 1950: 27). Tathlina Lake (60°32′N, 117°32′W) (Herrington, 1962: 30).



Distribution: Quebec to Alberta and southwestern Northwest Territories south to Florida, Texas and Mexico. Absent from the Maritime Provinces, New England, and most of the area west of the Rocky Mountains (but see Taylor, 1967). In the survey area it is most abundant in the Red River drainage area. Also in England, introduced.

Biology and Ecology: Of the 12 collections made during this survey, 3 are from large lakes, 5 are from rivers 100 to 300 feet wide, 3 are from rivers 50 to 100 feet wide, and 1 is from a river about 40 feet wide. Bottom sediment was predominantly of mud in all localities except Lake Winnipeg, where it was of sand. Vegetation was sparse to moderately abundant at each locality and in all lotic stations the current was moderate to slow.

Herrington (1962: 30) gives " large lakes, rivers, and sloughs " as the habitat of *Sphaerium transversum* and quotes Sterki that it is also found in rivers with strong currents on stony and rocky bottoms. Baker (1928b: 352) says " in rivers, ponds, and lakes usually in soft mud, on the surface or buried at different depths. " He also cites a locality with sand bottom.

Baker (loc. cit.) describes the soft parts as " whitish, greenish about the liver; most organs appear translucent; siphons long, united for the greater part of their length; anal (=excurrent) opening small, round, the end of the siphon turned upward when extended; branchial (=incurrent) opening larger, compressed laterally during extension; foot long, cylindrical, capable of great extension; other organs as in the group. "

Specimens from the Canadian Interior Basin and elsewhere were examined for enclosed young, with the following results:

Adult Length, mm	No. of Young	Length of Young, mm
Mouse River, 15 mi WNW of Mohall, N.D.		
12·4	34	2·1(25), 1·2(9)
Seine River, Grande Pointe, Man. (Aug. 9, 1964).		
10·4	23	1·4(7), 1·1(16)
Lake Erie, Sandusky Bay, Ohio (June 13–18, 1963).		
10·8	18	1·3(18)
10·0	10	1·7(3), 1·5(3), 1·3(4)
Detroit River, 4 mi S of Grosse Isle, Mich. (Sept. 16, 1963).		
12·0	14	2·0(4), 1·8(4), 1·5(3), 1·1(3)
Otter Creek, Garfield Co., Okla. (July 9, 1964).		
12·8	5	1·6(3), 1·1(2)

Genus *Pisidium* Pfeiffer

Pisidium Pfeiffer, 1821: *Naturgeschichte Deutscher Land-und Susswasser-Mollusken, 3*(Abt. *1*): 17, 123. Type species: *Tellina amnica* (Müller) by subsequent designation, Gray (1847: 185). *Pisidium* Pfeiffer has been placed on the Official List of Generic Names in Zoology (ICZN, Opinion, 335, 1955).

Shells very small (2 mm) to medium-sized (12 mm), ovate but asymmetrical in most species (with anterior produced and posterior abruptly rounded), slightly inflated to globose, and with umbones located posterio-dorsally. Only the anal siphon is developed, the branchial siphon being either rudimentary or represented by a mantle cleft. Gills four (as in *Sphaerium*) or posterior gills reduced or absent. Inner (pericardial) nephridial tube not looped but ascending directly upward. Animals monoecious and ovoviviparous.

Pisidium, like *Sphaerium*, is cosmopolitan. These are the "nut clams" and they occur in nearly all perennial and vernal waters up to and beyond the Arctic Circle. They are also eaten in large quantity by several fishes. Twenty-three species are now recognized from North America (Herrington, 1962; Heard, 1965) and 16 of these are known to occur in the Canadian Interior Basin. Geologic range: Upper Cretaceous to Recent.

Subgenus *Pisidium* Pfeiffer (*s. str.*)

Shell medium sized (6 to 12 mm) and relatively heavy. " Branchial siphon rudimentary or represented only by a slit in the fused mantle; large posterior (external)

PLATE 17. *Pisidium* (I)

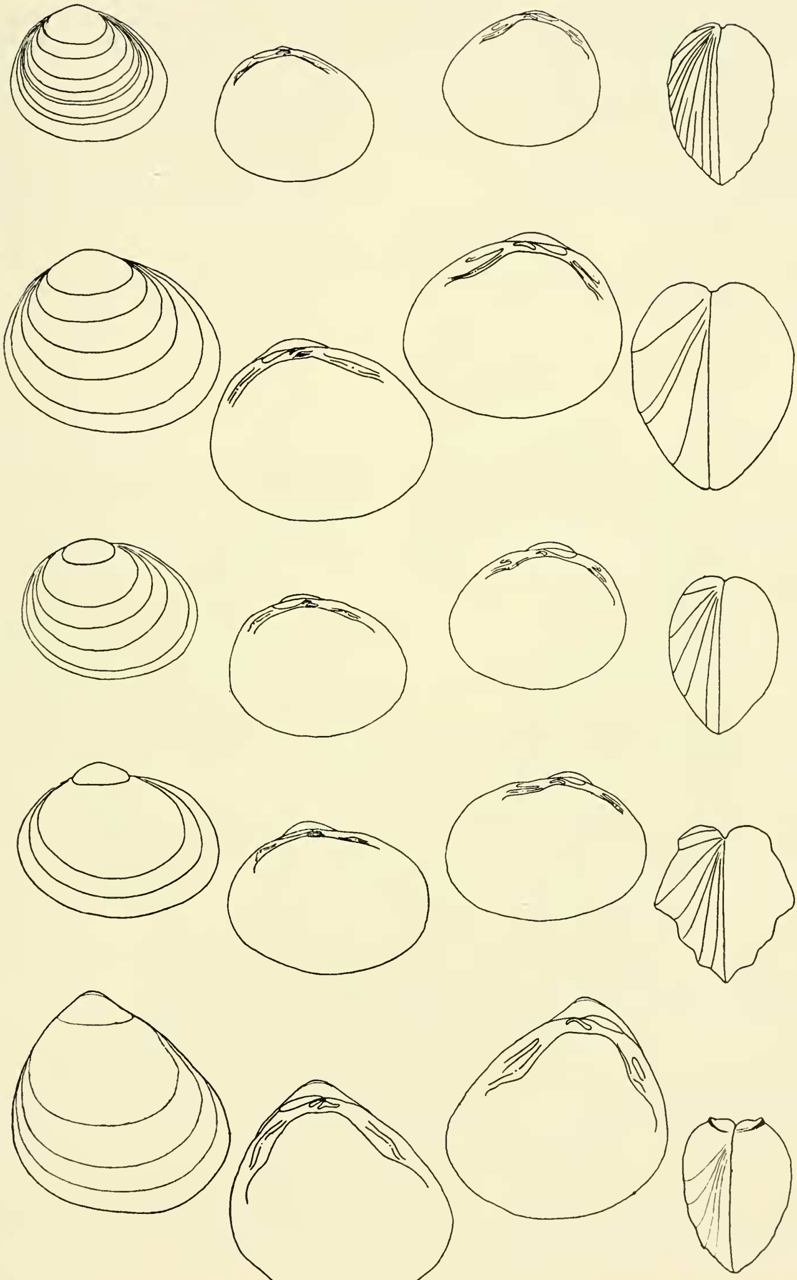
FIG. 1. *Pisidium idahoense*, Aberdeen Lake, Northwest Territories (NMC 15333, 7·3 mm) . . . . p 166.

FIG. 2. *Pisidium adamsi*, Murky Creek near Geraldton, Ontario (NMC 19141, 4·6 mm) . . . . . p 169.

FIG. 3. *Pisidium casertanum*, creek near Cochrane, Ontario (NMC 15580, 3·5 mm) . . . . p 171.

FIG. 4. *Pisidium casertanum*, Lac La Ronge, Saskatchewan (NMC 18908, 3·7 mm) . . . . p 171.

FIG. 5. *Pisidium compressum*, Woody River, near Swan River, Manitoba (NMC 14666, 4·0 mm) . . . . p 174.



1

2

3

4

5

gills present in addition to large anterior (internal) gills; posterior gills with ascending (inner) lamellae as well as descending (outer) lamellae; dorsal loop or lobe of the nephridia cleft. " (Heard, 1965: 383). " One medium (10 young) to large (20) litter produced each year for several years " (Heard, 1966: 86).

Three North American species belong in this subgenus, *Pisidium amnicum* (Müller), *P. dubium* (Say), and *P. idahoense* Roper. Only the last named occurs in the Canadian Interior Basin.

Pisidium (*Pisidium*) *idahoense* Roper
Plate 17, Fig. 1; Map 25.

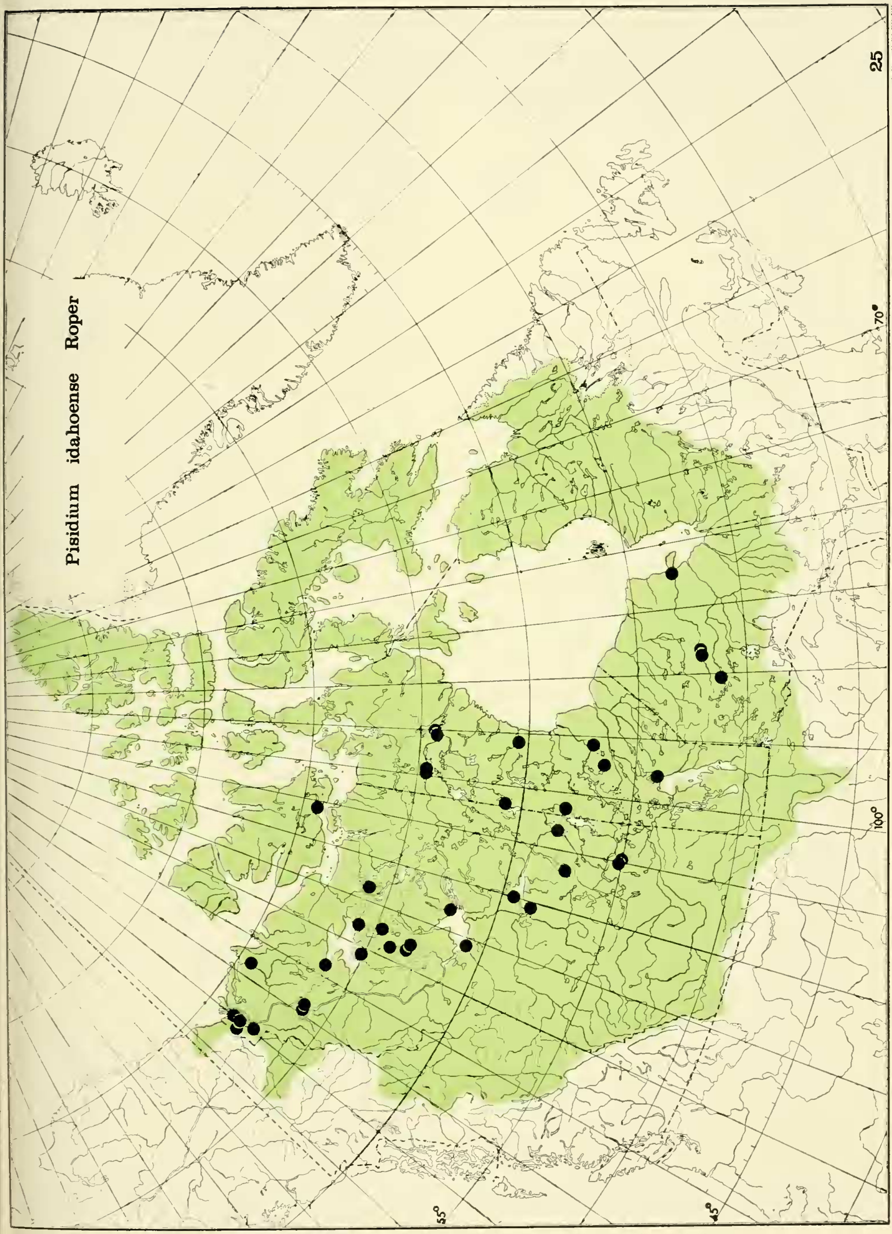
Pisidium idahoense Roper, 1890: *Nautilus*, *4*(8): 85. Type locality: " a muddy slough near Old Mission, in northern Idaho."

Diagnosis: Shell up to about ½ inch, moderately heavy to heavy, subovate, umbones low and posterior of centre, and concentric striae fine. Cusp of P2 is central.

Description: " Shell very large (some high, short, of great diameter, and very heavy; others high, of moderate diameter and weight, and longer); beaks low and broad; periostracum glossy; striae fine; dorsal margin very short and steeply rounded, joining anterior and posterior ends with very slight angle; anterior end a well-rounded, rather steep slope, joining ventral margin without angle; posterior end rounded; ventral margin well rounded; hinge moderately heavy, rather long and considerably curved; laterals in large specimens short; cusps rather blunt on top; cusp of A1 on distal side of centre or distal, of P1 distal, of A2 proximal or on proximal side of centre, of P2 central; cardinals slightly nearer anterior cusps; C2 very short and curved or, forming an inverted D; C4 much longer, straight or but slightly curved and directed toward cusp of P2 or a little inside; C3 rather long and considerably curved, about parallel with hinge-plate, centre frequently much thinner than ends, posterior end slightly more enlarged than the anterior. " (Herrington, 1962: 42).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Reindeer Lake, Brochet, Man.					
1	7·8	6·6	0·85	3·7	0·47
5	7·0	5·8	0·82	3·7	0·52
9	6·8	5·9	0·87	3·6	0·53
13	5·5	4·8	0·87	2·8	0·51
Aberdeen Lake, northwest side, N.W.T. (64°45′N, 100°00′W).					
1	7·8	6·5	0·83	4·0	0·51
5	7·2	6·1	0·85	3·7	0·51
9	6·7	5·9	0·88	3·7	0·55
13	6·4	5·7	0·89	3·4	0·53
McVicar Arm, Great Bear Lake, N.W.T.					
1	7·2	6·0	0·83	4·0	0·56
5	6·5	5·3	0·82	3·6	0·55
9	6·4	5·7	0·89	3·4	0·53
13	6·3	5·4	0·86	3·4	0·54


Pisidium idahoense Roper
25
70°
100°
55°
45°

Records:

Since more than 80 lots are available only marginal records are reported here. See Map 25. Ontario. Lake St. Joseph (51°05′N, 90°35′W). Hawley Lake (54°30′N, 84°39′W). Sachigo Lake (53°49′N, 92°08′W) (all 1961–63, Ont. Dept. Lands and Forests!).

Manitoba. Norway House, Little Playgreen Lake (1879, R. Bell!). Knee Lake, northern narrows (55°04′N, 94°45′W). Recluse Lake (56°55′N, 95°45′W). Reindeer Lake, Brochet (all this survey).

Saskatchewan. Lac la Ronge. Cree Lake (57°30′N, 106°30′W) (both 1945, D. S. Rawson!).

British Columbia. Cry Lake (from lake trout) (near 58°N, 129°W) (1962, S. D. MacDonald!).

Northwest Territories. Unnamed lake in Thlewiaza River (60°23′N, 95°45′W) (this survey). Baker Lake, about 12 mi S of Baker Lake settlement (from whitefish) (1962, E. W. Smith and W. L. Donahue, RCMP!). Keyhole Lake, Victoria Island (69°23′N, 106°14′W) (1959 Fish. Res. Bd.!). Aklavik (1957, Fish. Res. Bd.!).

Distribution: Vicinity of the Great Lakes north (on the west side of James Bay and Hudson Bay) to Victoria Island and the mouth of the Mackenzie River and west to the Aleutian Islands, British Columbia, Washington, and California. Apparently disjunct populations occur in the province of Prince Edward Island. Also in Sweden (NMC records).

Biology and Ecology: The 6 lots of *Pisidium idahoense* collected alive during this survey are all from large lakes. Depths ranged from 1 to 20 feet. Bottom deposits were various, from mud to gravel, with sand predominating, and aquatic vegetation was present at 4 localities and recorded as moderate at 2 and sparse at 2.

" Apparently, it lives in cool water—in large lakes, mountain regions, and the far North. In Great Slave Lake, Northwest Territories, it has been collected at a depth of 24 m..." (Herrington, 1962: 42). The several lots from Prince Edward Island indicate that in that province the species has become adapted to less severe environments. Similar habitats for *Pisidium idahoense* are also known in Michigan (Heard, 1962: 146).

Very little has been published on the anatomy or reproduction of this species. It is placed in *Pisidium* (*s. str.*), however, on conchological and anatomical grounds by Heard (loc. cit.). If the life cycle of *P. idahoense* is similar to that of other *Pisidium* (*s.str.*) species, i.e., *P. dubium* and *P. amnicum*, its life span can be expected to be about 3 years with a single brood of young born each year.

Remarks: The distribution of *Pisidium idahoense* is suggestive of Beringian survival during Wisconsin glaciation. The presence of apparently isolated populations on Prince Edward Island lends some support to the current theory that a Wisconsin glacial refugium may have existed somewhere in that region. It is unwise to attribute great significance to anomalous distribution patterns in *Pisidium*, however, since they are frequently transported by birds.

Subgenus *Cyclocalyx* Dall

" *Galileja* Costa " of authors but not of Costa, 1840. Original reference is O. G. Costa, 1840: *Fauna Siciliana, Mollusclii*, p 1, pl. 1: 2a, A.B. Type species: *Galileja tenebrosa* Costa, by monotypy. *Galileja tenebrosa* has been regarded by Woodward (1913: 2) and other authors as *Pisidium casertanum* (Poli) but Kuiper (1964) has shown that it is a marine species.

Euglesia Leach, 1852: *Molluscorum Britanniae Synopsis*. p 291 (not seen). Type species: *Euglesia henslowiana* (Sheppard) by monotypy. Kuiper (1962: 57) considers *E. henslowiana* a *nomen dubium*.

Cycladina Clessin, 1871: *Malak. Blätt.*, *18*: 189. Type species, by subsequent designation (Boettger, 1961: 240). *Pisidium nitidum* Jenyns. (Preoccupied by *Cycladina* Latreille 1827, and *Cycladina* Cantraine, 1835, both in Mollusca).

Rivulina Clessin, (*in* Westerlund), 1873: *Fauna Molluscorum terrestrium et fluviatilium* [etc.], *2*: 532. Type species *Pisidium supinum* Schmidt, by subsequent designation (Clessin, 1874).

(Preoccupied by *Rivulina* Fleuriau de Belleville, 1820, and *Rivulina* Lea, 1851, both in Mollusca).

Fossarina Clessin (*in* Westerlund), 1873: op. cit., p 535. Type species: *Pisidium obtusale* Pfeiffer, by subsequent designation (Clessin, 1874). Not *Fossarina* Adams and Angas, 1863 (Mollusca).

Pusillana Fagot, 1892: Histoire Malacologique des Pyrénées francaises et espagnoles. *Bull. Soc. Ramond de Bagnéres-de-Bigorre* (*Hautes-Pyrénées*), *27*: 148. Type species, by tautonomy, *Tellina pusilla* Gmelin. *T. pusilla* is a *nomen dubium* (Boettger, 1961: 237).

Roseana Fagot, 1892: op. cit., p 149. This name is not available since its original introduction is not in accordance with the ICZN Rules, Article 11F, i.e., it is not a singular noun but an adjective used in a plural sense. It also appears to be a vernacular name and as such it is doubly invalid.

Casertiana Fagot, 1892: op. cit., p 150. Not in accordance with Article 11F, also vernacular, and therefore invalid.

Henslowiana Fagot, 1892: op. cit., p 151. Not in accordance with Article 11F, also vernacular, and therefore invalid.

Cyclocalyx Dall, 1903: *Proc. biol. Soc. Wash.*, *16*: 7. Type species, by original designation, *Pisidium scholtzii* Clessin, 1873 [=*Pisidium obtusale* Lamarck, 1818 (fide Boettger, 1961: 24) =*P. obtusale* Pfr., 1821]. *Cyclocalyx* and the two following names are the earliest available names for this subgenus. Since *Cyclocalyx* has line precedence it is hereby selected as the valid name for the taxon under discussion.

Cymatocyclas Dall, 1903: op. cit., p 7. Type species by original designation, *Pisidium compressum* Prime.

Tropidocyclas Dall, 1903: op. cit., p 7. Type species by original designation, *Pisidium henslowanum* Sheppard.

Eupisidium Odhner, 1921: *J. Conchol.*, *16*: 222. Type species: *Pisidium personatum* Malm, by subsequent designation (Odhner, 1940: 3). For additional junior synonyms of *Cyclocalyx* and of other genus-group names in *Pisidium*, see Boettger (1961, 1962).

Shell medium-sized (3 to 6 mm) and with thick to thin walls. " Branchial siphon represented by a short slit in the fused mantle; small posterior gills usually present behind large anterior gills; posterior gills with ascending lamellae only; dorsal loop or lobe of the nephridia cleft. " (Heard, 1965: 383). In Central North America the species live only 1 year and bear 1 small to medium-sized litter (about 4 to 20 young).

Sixteen North American species are placed in this subgenus and all but 3 of these (*Pisidium henslowanum* Sheppard, *P. supinum* Schmidt and *P. ultramontanum* Prime) occur in the Canadian Interior Basin.

Pisidium (*Cyclocalyx*) *adamsi* Prime
Plate 17, Fig. 2; Map 26.

Cyclas nitida Mighels & Adams, 1842: *Boston J. natr. Hist.*, *4*: 39. Type locality: " Norway, Oxford Co., Me." (Not *Pisidium nitidum* Jenyns, 1832).

Pisidium adamsii Prime, 1852: *Boston J. natr. Hist.*, *6*: 352 (new name for *Pisidium nitidum* (Mighels & Adams) preoccupied).

Diagnosis: Shell up to about 5/16 inch long, rather heavy, inflated, with long sloping anterior end, heavy lateral teeth, and with C4 directed toward the cusp of P2 or slightly below.

Description: " Shell very large and considerably inflated; beaks broad and full, many specimens with a flattening best seen in juvenile and nepionic shells; striae rather heavy and uniformly spaced; periostracum very dull; dorsal margin long and gently curved; anterior end rather steep, the slope slightly curved; posterior end truncate and vertical; ventral margin long and gently curved. Hinge long, openly curved and heavy; laterals heavy with heavy cusps, broad on top. Cusp of A1 on the distal side of centre; cusps of P1 distal, of A2 proximal, of P2 on distal side of centre; cardinals central or on anterior side of centre; C3 long, considerably curved, its posterior end a little enlarged; C4 as long as, or longer than C2, slightly curved and usually not directed toward interior of shell, but toward cusp of P2 or just inside of it; C2 varies in length, greatly curved or bent. " (Herrington, 1962: 30).

The above is a description of Ontario

specimens (H. B. Herrington, pers. comm. Oct. 24, 1968). These differ from Prime's specimens in that Ontario specimens have their anterior ends less rounded and correspond with *Pisidium adamsi affine* Sterki.

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Cormorant Lake, Man. (54°14′N, 100°49′W).					
1	4·7	4·0	0·85	3·3	0·70
5	3·3	2·7	0·89	2·0	0·61
9	3·0	2·5	0·83	1·7	0·57
13	2·7	2·2	0·81	1·5	0·56
Winisk River, 15 mi S of Winisk, Ont.					
1	4·7	3·9	0·83	3·0	0·64
5	4·6	3·8	0·83	2·8	0·61
9	4·4	3·7	0·84	2·8	0·64
13	4·1	3·4	0·83	2·3	0·56
Klotz Lake, 30 mi E of Longlac, Ont.					
1	4·5	3·5	0·78	2·5	0·56
5	4·4	3·4	0·77	2·7	0·61
9	4·3	3·6	0·84	2·5	0·58
13	4·0	3·2	0·80	2·4	0·60

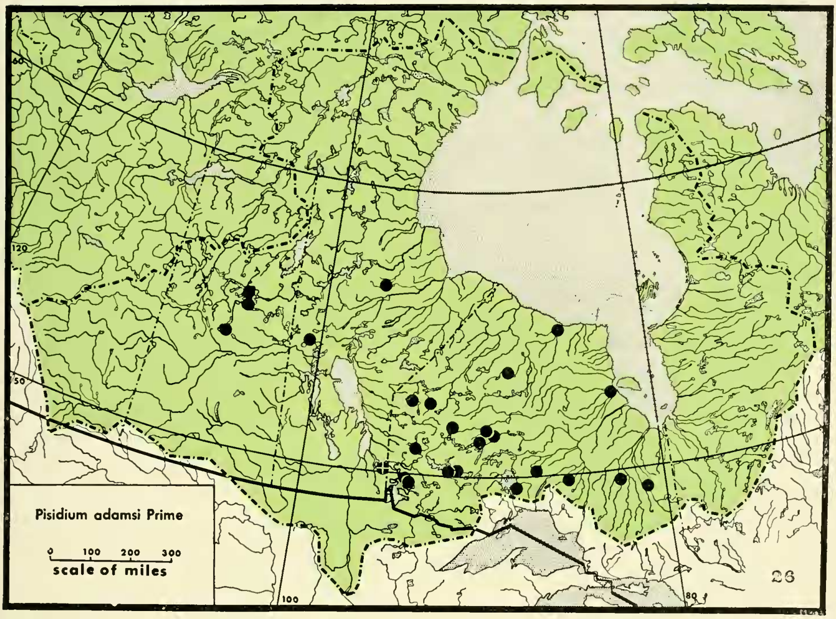
Records:

Ontario. Abitibi River 17 mi N of Cochrane. Small lake 11 mi ESE of Kapuskasing. Klotz Lake, 30 mi E of Longlac. Murky Creek, 27 mi N of Geraldton. Small pond near Lake Nipigon, 20 mi S of Beardmore. Medcalfe Lake, north end, 63 mi N of Savant Lake. Lake St. Joseph, Rat Rapids (all this survey). Cat Lake (51°40′N, 91°50′W), (1929, A. R. Cahn!). Fitchie Lake (50°38′N, 90°32′W) (Baker & Cahn, 1931: 47). Attawapiskat River, 6 mi W of Attawapiskat. Winisk River, 15 mi S of Winisk. Shibogama Lake (53°31′N, 88°35′W). Deer Lake, Deer Lake settlement (52°09′N, 94°00′W). North Spirit Lake, at outlet (52°31′N, 93°02′W). "Sturgeon River" [Marchington River], 1 mi W of Superior Junction. Pelican Lake, Sioux Lookout. Stone River, 11 mi S of Red Lake. Chadwick Lake, 15 mi and 16 mi E of Kenora (2 localities) (all this survey).

Manitoba. Lake Brereton (Mozley, 1938: 121). Cormorant Lake (1906, W. McInnes!). Limestone Lake, east end (56°35′N, 96°00′W) (this survey).

Saskatchewan. Bittern Creek, 15 mi N of Waskesiu Lake (this survey). Lac la Ronge (1954, D. S. Rawson!). Lynx Lake, 29 mi N of La Ronge (this survey).

Distribution: Nova Scotia (NMC records) west to Saskatchewan and Montana and south to Florida, Alabama and Colorado. Not recorded from far-



western North America or the south-central United States.

Biology and Ecology: The 21 lots of *Pisidium adamsi* collected during this survey came from the following habitats: 7 lots are from large lakes, 4 from small lakes, 1 from a permanent pond, 5 from rivers over 100 feet wide, 1 from a river 50 to 100 feet wide, and 3 from streams 25 to 50 feet wide. Current was moderate, slow, or not perceptible in the river and stream localities. Aquatic vegetation was present (thick, moderate, or sparse) and bottom deposits were of all types (mud predominating) at all localities.

Herrington (1962: 31) gives small lakes, ponds, rivers, and (rarely) creeks with " a preference for mud and decaying vegetable matter " as the habitat for *Pisidium adamsi.* Baker (1928b: 386) also records it from large lakes. The present data confirm these statements except that the species is also common in permanent streams of several sizes.

Heard (1964: 47) examined 15 specimens of *Pisidium adamsi* collected on June 3, 1962 from Ore Creek, Livingston County, Michigan and found them all to contain shelled young. These embryos numbered from 10 to 66 (mean 25·5) in single adults.

Pisidium (*Cyclocalyx*) *casertanum* (Poli)
Plate 17, Figs. 3, 4; Map 27.

Cardium casertanum Poli, 1795: *Testacea utriusque Siciliae* [etc.]. Parma, *2*: 65. Reprinted in Ellis, 1940; *Proc. malacol. Soc.*, London, *24*: 58. Type locality: " in rivuli Alveo per regium Casertae " [in stream beds throughout the vicinity of Caserta, Italy]. *Cardium casertanum* Poli has been placed on the Official List of Specific Names in Zoology (ICZN Opinion 587, 1961).

Pisidium abditum Haldeman, 1841: *Proc. Acad. natr. Sci. Philad.*, *1*: 53. Type locality: "Springs in Lancaster Co., Pennsylvania."

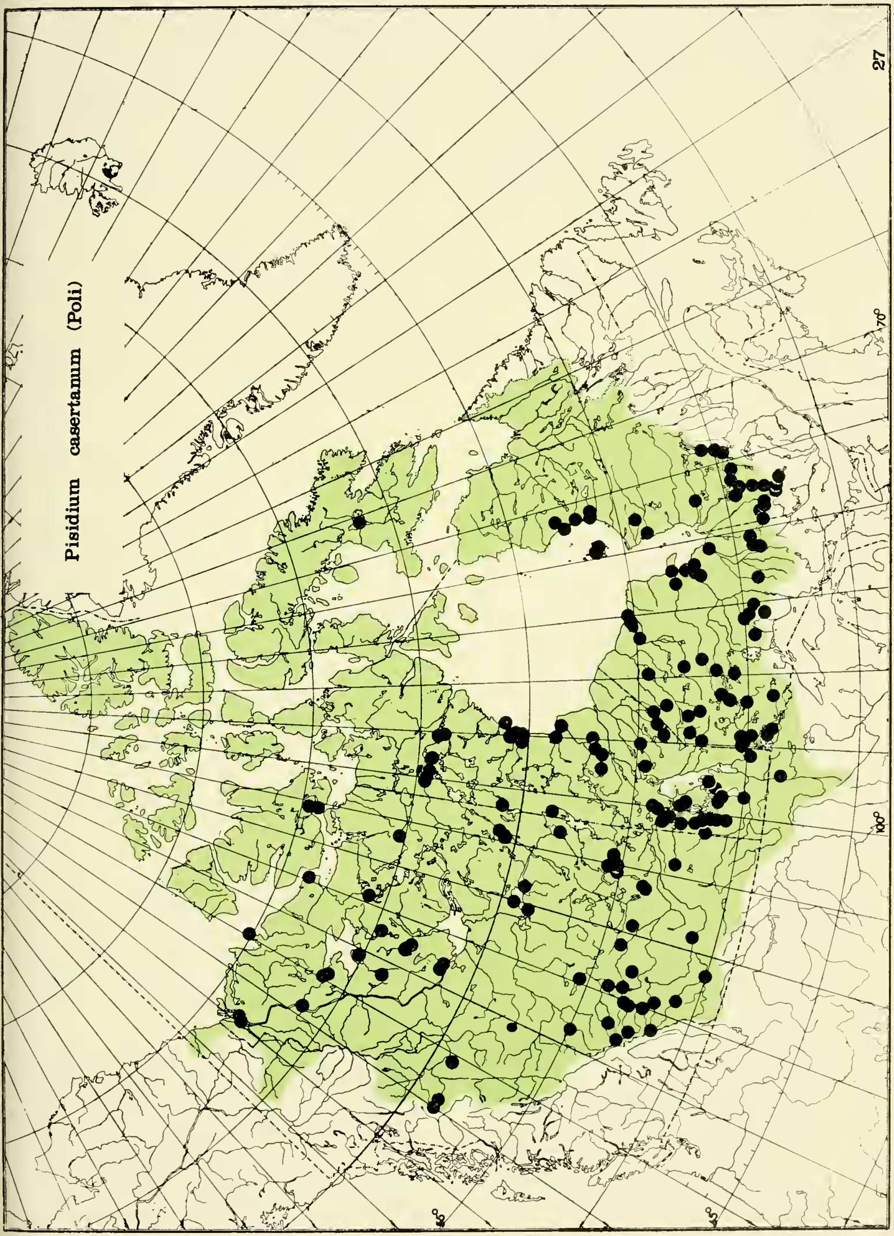
For additional synonyms see Herrington, 1962: 33.

Diagnosis: Shell up to ⅓ inch long (most specimens ⅙ inch), of medium thickness, long, triangular ovate, with wide, posterior-of-centre umbones, medium-glossy periostracum, and moderately short hinge. This is the most common species of *Pisidium*.

Description: "The average shell is rather long in outline. Shell of moderate weight; beaks subcentral to a little farther back, not high; striae rather fine; periostracum moderately dull to slightly glossy; dorsal and ventral margins... gently curved, dorsal margin usually joins ends with slight angles; anterior end moderately long and rounded; posterior end truncate; hinge-plate moderately long, fairly broad, laterals distinct, but not long; cusps on laterals rather sharp; cusp of A1 on distal side of centre, of A2 proximal or on proximal side of centre, of P2 on distal side of centre; P1 and P3 short, cusps distal; cardinals near anterior cusps; C3 slightly curved and somewhat enlarged at posterior end, C2 usually an inverted D, C4 thin and more or less curved, directed toward interior of the shell." (Herrington, 1962: 33).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Char Lake, near Richmond Gulf, northern Que.					
1	4·5	4·0	0·89	2·9	0·65
5	3·6	3·1	0·86	2·4	0·67
9	3·4	2·9	0·85	2·0	0·59
13	3·0	2·7	0·90	1·9	0·63
Small lake 10 mi N of Sidney, Man.					
1	4·9	4·0	0·82	3·2	0·65
5	4·5	4·0	0·89	3·1	0·69
9	4·3	3·6	0·84	3·0	0·70
13	4·0	3·3	0·82	2·6	0·65
Fossil Lake, N.W.T. (66°17′N, 128°55′W).					
1	3·8	3·3	0·87	2·6	0·68
5	3·7	3·2	0·86	2·6	0·70
9	3·6	3·0	0·83	2·5	0·69
13	3·5	3·1	0·89	2·7	0·77


Pisidium casertanum (Poli)
27
70°
100°
PRODUCED BY THE SURVEYS AND MAPPING BRANCH DEPARTMENT OF ENERGY, MINES AND RESOURCES

Records:

More than 300 lots are available from the research area and therefore only marginal records are given. See Map 27.

Quebec, Ontario, Minnesota, North Dakota, Manitoba, Saskatchewan, and Alberta. Abundant throughout.

Northwest Territories. Nettilling Lake, Baffin Island (1956, D. R. Oliver!). Greiner Lake, Victoria Island (1959, Fish. Res. Bd.!). Cape Parry (1962, G. Abrahamson!).

Distribution: According to the literature this species is nearly cosmopolitan. It occurs throughout Eurasia, in most (perhaps all) of Africa, in Australia, New Zealand, and Tasmania, throughout South America, Central America, and North America as far north as the southern tier of Arctic Islands (see " Records ").

Biology and Ecology: The 111 lots of *Pisidium casertanum* collected during this survey are from the following habitats: 38 from large lakes, 11 from small lakes, 5 from permanent ponds, 3 from muskeg, 2 from ditches, 1 from a small pool among rocks, and 51 from rivers and streams of all widths from 500 feet to under 10 feet. Vegetation was present at all but 9 localities but of varying abundance. Bottom deposits were various but predominantly of mud. Current varied among lotic stations although it was slow at most.

Herrington (1962: 34) writes: " *P. casertanum* has succeeded in adapting itself to a wide variety of habitats. One finds it in bog ponds, ponds, swamps that dry up for several months of the year, swamp-creeks, creeks with considerable current, rivers, and lakes, including the Great Lakes. This is by far the most common *Pisidium*. "

Heard (1965: 395) showed that *Pisidium casertanum* in Michigan contains embryos only during late spring and summer, that spermatogenesis and oogenesis occur throughout the year, but that mature gametes are most abundant during the fall and winter. Litter size in 2 Michigan populations varied from 1 to 32 and 2 to 42, with means of 8·5 (N=133) and 16·3 (N=32) respectively. Life span in Michigan is 1 year, but according to Odhner (in Heard, op. cit.), life span in Swedish populations exceeds this.

Remarks: Ellis (1940: 57) quotes a statement from a manuscript by Stelfox which is particularly pertinent, viz., " In attempting to identify all Pisidia, and most especially *P. casertanum*, it is well to bear in mind at all times that we need not expect to find the hinge characters normal in a shell that is very thin, or very thick, or in any way abnormal. In thin shells the cardinals will be less curved, in thick shells more strongly curved, moreover the thicker and more trigonal the shell becomes, the shorter will the ligament be. When we consider that *P. casertanum* will live in almost all conceivable habitats it will readily be understood that its range of variation is likely to be great, but it is the protean nature of the species that renders this variation almost miraculous and if sufficient material be collected and studied, forms of this species will be found that closely resemble some forms of most of our other species. "

Pisidium (*Cyclocalyx*) *compressum* Prime
Plate 17, Fig. 5; Map 28.

Pisidium compressum Prime, 1852: *Proc. Boston Soc. natr. Hist.*, *4*: 164. Type locality: " Fresh Pond, near Cambridge [Mass.]."

Diagnosis: Shell about $\frac{1}{8}$ inch long, solid, subtriangular, and with a dull periostracum. In most specimens the umbones are flattened near their apices and farther back each umbone bears a prominent, concentric ridge (an " appendicula "). Common.

Description: "Shell of medium size, heavy, varying from short and high to moderately long; beaks rather prominent, quite far back, narrow and usually with ridges; striae of medium coarseness to moderately fine; periostracum dull; dorsal margin short and round; anterior end...rather steep... ventral margin long (three times that of the dorsal) and considerably curved, ...posterior end broadly rounded, vertical or slightly cut under; hinge long, heavy, and moderately to steeply curved; laterals rather short, being incorporated into the hinge-plate; A3 and P3 tend to curve around the pit of the sulcus; cusps blunt on top; cusp of A1 distal, of P1, A2 and P2 central or on distal side of center; cardinals central; C3 short, considerably curved, posterior end much the larger; C2 short and stout like an inverted D; C4 rather short, slightly curved, and directed toward cusp of P2; space between posterior end of C2 and C4 considerable." (Herrington, 1962: 35).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Duparquet River, 3 mi N of Rapide Danseur, Que.					
1	3·3	3·1	0·94	2·3	0·70
5	2·9	2·6	0·90	2·0	0·69
9	2·8	2·5	0·89	1·9	0·68
13	2·6	2·3	0·89	1·7	0·65
Attawapiskat River, 8 mi W of Attawapiskat, Ont.					
1	3·4	3·1	0·91	2·3	0·68
5	3·3	2·8	0·85	2·1	0·75
9	2·9	2·5	0·86	1·7	0·68
13	2·7	2·2	0·81	1·7	0·63
Blindman River, 5 mi N of Red Deer, Alta.					
1	3·4	3·0	0·88	2·2	0·65
5	3·2	3·1	0·97	2·2	0·69
9	3·0	2·7	0·90	2·0	0·67
13	2·9	2·7	0·93	1·7	0·59

Records:

Since more than 110 lots of this species are available from the research area only marginal records are listed here. All localities are plotted on Map 28.

Quebec. Middle Fork, Roggan River, 73 mi SSW of Poste de la Baleine (Great Whale River). Eastmain River, 16 mi E of Eastmain and 1 mi above rapids (both this survey).

Ontario. Albany River near Fort Albany (4 collections). Attawapiskat River near Attawapiskat (5 collections). Shamattawa River and Winisk River, 15–22 mi S of Winisk (3 collections). Lake at source of Shell Brook (55°20′N, 87°17′W). Stull Lake, at outlet (54°29′N, 92°37′W) (all this survey).

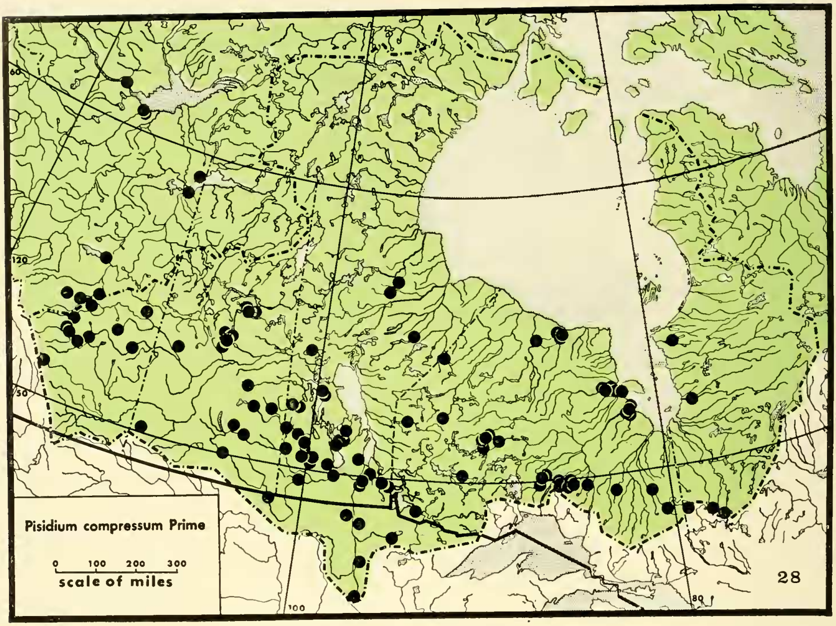
Manitoba. Knee Lake, northern narrows (55°04′N, 94°45′W). Recluse Lake, Little Churchill River (56°55′N, 95°45′W). Limestone Lake, east end (56°35′N, 96°00′W) (all this survey).

Saskatchewan. Lac la Ronge (whitefish stomachs, 1948, D. S. Rawson! also this survey).

Alberta. "The Willows", Lake Athabasca (1945, D. S. Rawson!). Second Vermilion Lake, Banff (this survey).

Northwest Territories. Mouth of Hay River (ca. 1917, E. J. Whittaker!). "Little Lake" [Mills Lake] (1917, E. M. Kindle!) (both single valves and possibly subfossil).

United States. Lake Traverse, Brown's Valley Minn. (this survey).



Distribution: Prince Edward Island northwest to the vicinity of southern Hudson Bay (both sides, this survey), the Mackenzie River near Great Slave Lake, Alaska, and south throughout the United States and into Mexico (Herrington, 1962: 35).

Biology and Ecology: The 82 lots of *Pisidium compressum* collected during this survey are from the following habitats: 26 are from large lakes, 6 from small lakes, 2 from permanent ponds, 19 from rivers over 100 feet wide, 11 from rivers 50 to 100 feet wide, 8 from streams 25 to 50 feet wide, 6 from streams 10 to 25 feet wide, and 4 from streams less than 10 feet wide. Vegetation was present at all stations but 2, but in varying abundance. Bottom deposits were of all types, with mud most frequently met. Current velocities in lotic habitats were predominantly slow or moderate but at 5 stations current was rapid and at 4 it was not perceptible. *P. compressum* was dredged in down to 8 m depth in Lac la Ronge.

Under " Habitat " Herrington (1962: 35) writes " creeks, rivers, and lakes. It has a preference for sandy bottoms with vegetation, and shallow water. " Depths to 20 m are also cited. Data from this survey agree with Herrington's statement although *Pisidium compressum* also occurred in 2 ponds, each of about ½ acre area.

Heard (1965: 395) has shown that *Pisidium compressum* " *sensu lato* " in Michigan contained spermatozoa and ova throughout the year. Average litter size was 15·7 and 20·3 (2 years, in late spring) for " *P. c. illinoisense* " and 2·6 (in middle and late summer) for " *P.c. pellucidum* ". Range of

litter size was 1 to 42 during each year for the former population and 1 to 6 for the latter, and only 1 litter a year is produced in the species. Parasitism by trematodes is suggested as the probable explanation for the low embryo yield in the latter population. *P. compressum* lives only 1 year in common with the other species of the subgenus *Cyclocalyx* which have been studied (Heard, 1962: 405).

Pisidium (*Cyclocalyx*) *equilaterale* Prime
Plate 18, Fig. 1; Map 29.

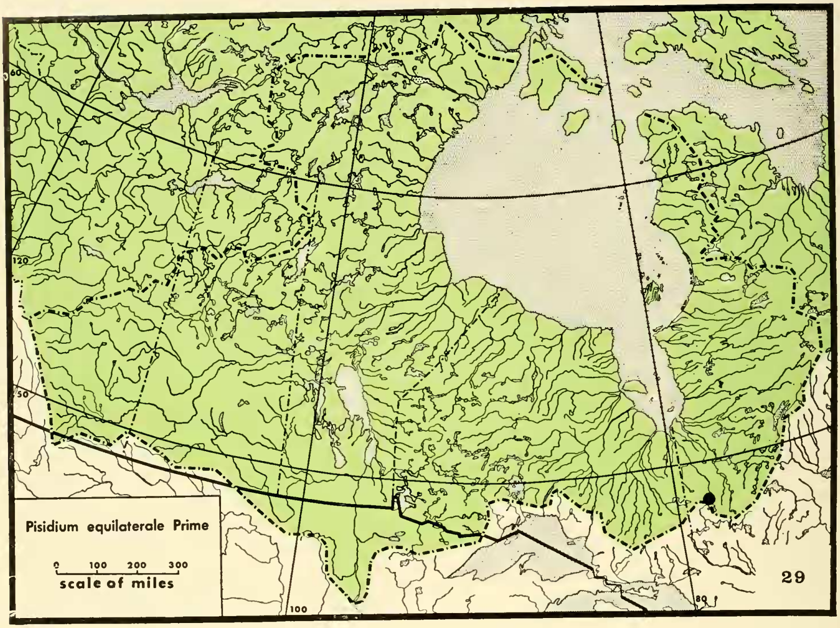
Pisidium equilaterale Prime, 1852: *Boston J. natr. Hist.*, *6*: 366, pl. 12: 23–25. Type locality: " in a clay pit near Augusta, Me."
" *Pisidium aequilaterale* Prime " of authors, e.g., Herrington, 1962: 31.

Diagnosis: Shell about ⅛ inch long, solid, slightly inflated, nearly round when viewed internally, and with large, swollen, subcentral umbones.

Description: " Shell medium size, short, heavy; beaks central, large, broad, very high, full, and usually flattened a bit on top; striae moderately fine but distinct; periostracum moderately glossy; dorsal margin rather long and somewhat steeply rounded; ventral margin almost as long, but not quite as steeply rounded as dorsal; anterior end short and very steep,...posterior end round, ...hinge well curved, long, almost full length of shell; hinge-plate heavy; laterals heavy, rather short, cusps blunt on top; cusps of A1 distal, of P1 on distal side of center or central, of A2 distal or on distal side of center, of P2 central; cardinals central, C3 steeply curved, anterior end rather slim, C2 varies in size, C4 almost straight, directed toward cusp of P2; space between C2 and C4 is a slit directed toward cusp of P2. When a single valve is viewed from the inside, *Pisidium aequilaterale* comes nearest to being round in outline of any of our *Pisidium*. " (Herrington, 1962: 31).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Outlet of Lac Gauvin, 4½ mi WNW of Amos, Que. (July 29, 1963).					
1	2·4	2·0	0·83	1·5	0·62
2	2·1	1·8	0·86	1·3	0·62
Lagoon, Carp River, Fisher Township, Ont. (near Lake Superior) (July 7, 1965).					
1	2·8	2·4	0·86	1·8	0·64
2	2·2	1·9	0·86	1·4	0·65
Bagwa Picnic Area, 10 mi W of Mattawa, Ont., (July 11, 1961).					
1	2·9	2·5	0·86	1·7	0·59
2	2·8	2·4	0·86	1·7	0·61
3	2·6	2·2	0·85	1·6	0·61
4	2·6	2·2	0·85	1·5	0·58
5	2·6	2·1	0·81	1·5	0·58



Records:

Outlet of Lac Gauvin, 4½ mi WNW of Amos, Abitibi Co., Que. (Harricanaw River system) (2 specimens this survey).

Records close to the Hudson Bay drainage area but just south of it are: small creek NW of St. Felicien, Que.; Lake at Bagwa picnic grounds 10 mi W of Mattawa, Ont.; and lagoon near mouth of Carp River at Lake Superior (46°57′N, 84°35′W), Ont. (all this survey).

Distribution: New Brunswick (Herrington & Reigle, 1967: 110) west through south-central Quebec and Ontario to the vicinity of eastern Lake Superior (this survey) and south to Virginia, Pennsylvania, and Illinois (Herrington, 1962: 32). Previous records from Michigan which are doubted by Heard (1962:142) on zoogeographic grounds may be correct.

Biology and Ecology: According to Herrington (1962: 32) *Pisidium equilaterale* occurs in "creeks, rivers, and lakes (and) prefers small weeds on a fine, sandy bottom. Almost all specimens are from igneous rock formations."

The outlet of Lac Gauvin, cited above, was about 8 feet wide and 1 foot deep on July 29, 1963, and had a sand and mud bottom with thick, submersed vegetation. The other localities cited above are a small creek, a small lake, and a lagoon at the mouth of a river. These limited data support Herrington's statement.

No information is available on the anatomy or reproduction of this species.

Remarks: The original spelling by Prime i.e., *Pisidium equilaterale*, has been reinstated for this species.

Pisidium (*Cyclocalyx*) *fallax* Sterki
Plate 18, Fig. 2; Map 30.

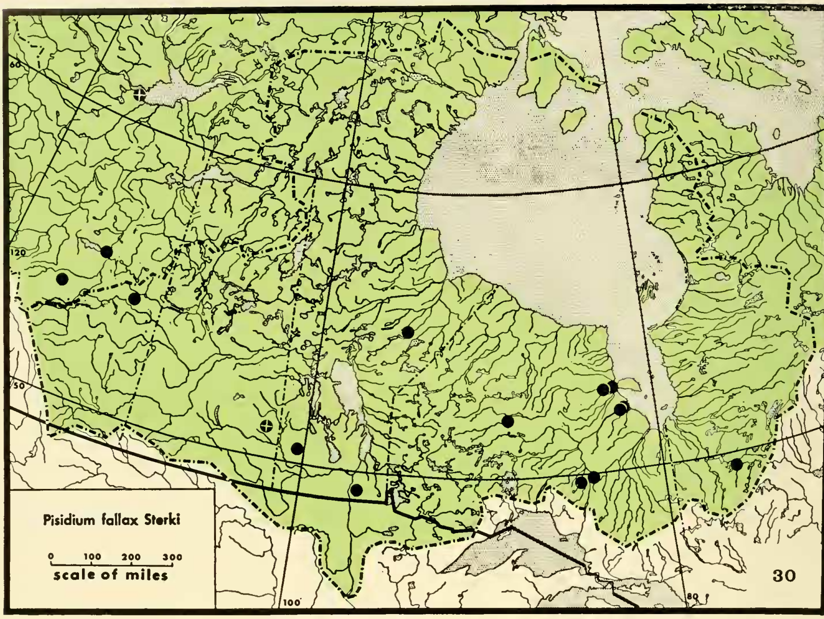
Pisidium fallax Sterki, 1890: *Nautilus*, *10*(2): 20. Type locality: "Tuscarawas River and Sugar Creek, Ohio."

Diagnosis: Length up to about $\frac{1}{8}$ inch, relatively compressed and of medium thickness, triangular-ovate, with low umbones and dull periostracum. Cusp of anterior lateral tooth of left valve abrupt, prominent, and twisted toward interior of body cavity.

Description: "Shell small to medium size, short, usually of little diameter, walls of medium thickness; beaks subcentral, some fairly plain, some flattened a little and some having low ridges; striae moderately coarse; periostracum very dull; dorsal and ventral margins slightly curved; anterior end rather short, steep, the slope more or less curved; posterior end truncated, vertical; hinge very broad and moderately long; laterals not very long; cusps mostly low and not very sharp; cusps of A1 central or on proximal side of center, usually leaning inward (the hinge-plate is much widened here); cusps of P1 central, of P2 central or on proximal side of center, of A2 central or on proximal side of center, not at center of hinge-plate but well inside, which gives it the appearance of a twist so that it is not parallel with the shell margin or directed across it, but directed somewhat inward. This accounts for the great width at A1. A1 and A3 not parallel, but somewhat V-shaped. The cardinals are subcentral to near the anterior cusps; C2 an inverted D; C4 straight or a little curved and directed slightly inside cusps of P2; C3 mostly short, much curved and directed across the hinge-plate, but it varies considerably." (Herrington, 1962: 38).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Inlet of Albany River, 7 mi W of Fort Albany, Ont.					
1	2·5	2·2	0·88	1·5	0·60
5	2·4	2·0	0·83	1·2	0·50
9	2·2	1·9	0·86	1·2	0·55
13	2·1	1·8	0·86	1·2	0·57
Attawapiskat River, 6 mi W of Attawapiskat, Ont.					
1	2·5	2·0	0·80	1·4	0·56
5	2·3	1·4	0·83	1·2	0·52
9	2·2	1·9	0·86	1·2	0·55
13	2·1	1·8	0·86	1·2	0·57
Driftwood River, 2½ mi N of Spurfield, Alta.					
1	3·0	2·6	0·87	1·8	0·60
2	2·6	2·3	0·89	1·6	0·62
3	2·4	2·1	0·88	1·3	0·54
4	2·2	1·8	0·82	1·1	0·50



Records:

Quebec. Small river 9 mi NE of Demaraisville (this survey).

Ontario. Kabinakagami River (50°11′N, 85°15′W) (1967, B. C. McDonald!). Nagagami River, 40 mi W of Hearst. Mouth of Stooping River, 12 mi W of Fort Albany. Inlet of Albany River, 7 mi W of Fort Albany (all this survey). "Ojiski" [Ozhiski] Lake (52°01′N, 88°30′W) (1904, W. McInnes!). Monument Channel, at portage, 20 mi W of Attawapiskat. Attawapiskat River, 6 mi W of Attawapiskat (both this survey).

Manitoba. Rat River, 1½ mi S of La Rochelle. Minnedosa River, 10 mi NNW of Minnedosa (both this survey). Knee Lake (55°03′N, 94°40′W) (1905, [E. A. Preble!]).

Saskatchewan. Whitesand River near Theodore (Mozley, 1938: 120).

Alberta. Caché Lake, at outlet, 2 mi W of Spedden. Trout Creek, 14 mi NE of Edson. Driftwood River, 2½ mi N of Spurfield (all this survey).

Northwest Territories. Great Slave Lake, west end (Herrington, 1950: 26).

Distribution: Sporadically distributed from Maine (NMC records) northwest to the vicinity of western James Bay and beyond to Great Slave Lake, west in southern Canada and northern United States to Alberta and Washington, and south to New Jersey. It is also recorded from Alabama (Herrington, 1962: 39).

Biology and Ecology: The 11 lots of *Pisidium fallax* collected during this survey are all from rivers, viz., 5 from rivers over 100 feet wide, 2 from rivers 50 to 100 feet wide, and 4 from rivers 25 to 50 feet wide. Aquatic vegetation occurred in at least 9 localities (its presence or absence was not recorded at 2) and varied from thick to sparse. Current varied from rapid to not discernible and bottom deposits were various, with mud present at 9 localities and gravel at 7. Mud was the sole

substrate at only 1 locality: Caché Lake, Alberta, at the outlet.

These data are only partly in agreement with Herrington (1962: 39) who states that this species " has a preference for coarse sand or gravel, even sandy gravel in cracks on a flat rock bottom... it appears to like water in motion, i.e., large creeks, rivers, or lakes and bays where there is considerable wave action. "

The reproduction and life history of this species in Michigan has been discussed by Heard (1965: 386-395). *Pisidium fallax* lives for only 1 year. Germ cells occur in greatest abundance during the winter and the percentage of individuals which are gravid reaches a peak (96% in the population studied) in May. The average number of embryos per adult also reaches a peak (8·6) in May.

Pisidium (*Cyclocalyx*) *ferrugineum* Prime
Plate 18, Fig. 3; Map 31.

Pisidium ferrugineum Prime, 1852: *Proc. Boston Soc. natr. Hist.*, *4*: 162; 1852: *Boston J. natr. Hist.*, *6*: 362, pl. 12: 8–10. Type locality: " found at Salem, and rarely at Cambridge [Massachusetts]."

Diagnosis: Shell about 1/10 inch long, subovate, thin, inflated, and variable in shape. Some specimens are partly covered with a reddish deposit. The cardinal teeth are not central but are close to the anterior cusps and the cusps of A2 and P2 are prominent, unusually elevated, and pointed.

Description: " Shell small, usually much inflated, walls thin; beaks subcentral, tubercular, plain, or even low and broad; they usually do not blend into shell readily; striae coarse to faint; periostracum glossy; dorsal margin rounded, length variable; ventral margin rounded much as dorsal, but longer; posterior end rounded, vertical or even extending outward near ventral margin, rarely cut under; anterior end with greater or less degree of slope depending on length of dorsal margin, joins ventral margin without an angle; hinge-plate narrow and light; laterals short with rather pointed cusps; sometimes inner laterals of right valve are curved outward at their outer ends; cusps of A1 central or on distal side of center, of A2 central or on proximal side of center, of P2 fairly distal (cusps of A2 and P2 are short and high with near-vertical ends); cardinals straight or slightly curved, very small and near anterior cusps, particularly in specimens with short dorsal margin; C2 and C4 roughly parallel with each other, but not with the hinge-plate as the space between them more often runs diagonally across it. " (Herrington, 1962: 39).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Lac Villebon, 12 mi S of Louvicourt, Que.					
1	2·6	1·6	0·63	2·2	0·85
5	2·4	1·5	0·63	2·0	0·83
9	2·2	1·2	0·55	1·8	0·82
13	2·0	1·2	0·60	1·8	0·90

Spec. No.	L	H	H/L	W	W/L
Recluse Lake, Man. (56°55′N, 95°45′W).					
1	2·8	2·2	0·79	2·5	0·89
5	2·6	2·0	0·77	2·1	0·81
9	2·3	1·7	0·74	1·8	0·78
13	2·2	1·7	0·77	1·9	0·86
Lake Athabasca, Camsell Portage, Sask.					
1	2·5	1·7	0·84	2·1	0·68
3	2·4	1·6	0·83	2·0	0·67
5	2·3	1·7	0·83	1·9	0·74
9	1·6	1·0	0·94	1·5	0·63

Records:

More than 60 lots of this species are available from the research area so only marginal records are listed. See Map 31.

Quebec. Lake Aigneau (57°10′N, 70°35′W) (1955, D. R. Oliver!). Rivière á la Perche, 48 mi NE of Chibougamau. Lac Dubuisson, 4 mi NW of Val d'Or (both this survey).

Ontario. Attawapiskat River, 6 mi W of Attawapiskat. Lake at source of Shell Brook (55°20′N, 87°17′W) (both this survey).

Northwest Territories. Aberdeen Lake, northwest side, from whitefish stomach (64°45′N, 100°00′W) (1961, Elizabeth Macpherson!). Keyhole Lake, Victoria Island (69°23′N, 106°14′W) (1959, Fish. Res. Bd.!). Aklavik, Mackenzie River (1957, Fish. Res. Bd.!).

Alberta. Inlet of Third Vermilion Lake, Banff (this survey).

Distribution: New Brunswick northwest to Ungava, Victoria Island, and the Mackenzie River mouth; west to British Columbia, Washington and Utah, and south to New Jersey. Also Europe.

Biology and Ecology: The 32 lots of *Pisidium ferrugineum* collected during this study are from the following habitats: 12 are from large lakes, 6 from small lakes, 1 from a perennial pond, and 13 from streams of various widths (from over 100 to under 10 feet). Aquatic vegetation was noted at all localities except 1 and varied widely in abundance. Bottom deposits also varied, with mud predominating, followed closely by sand. Current in all stream habitats was slow to moderate.

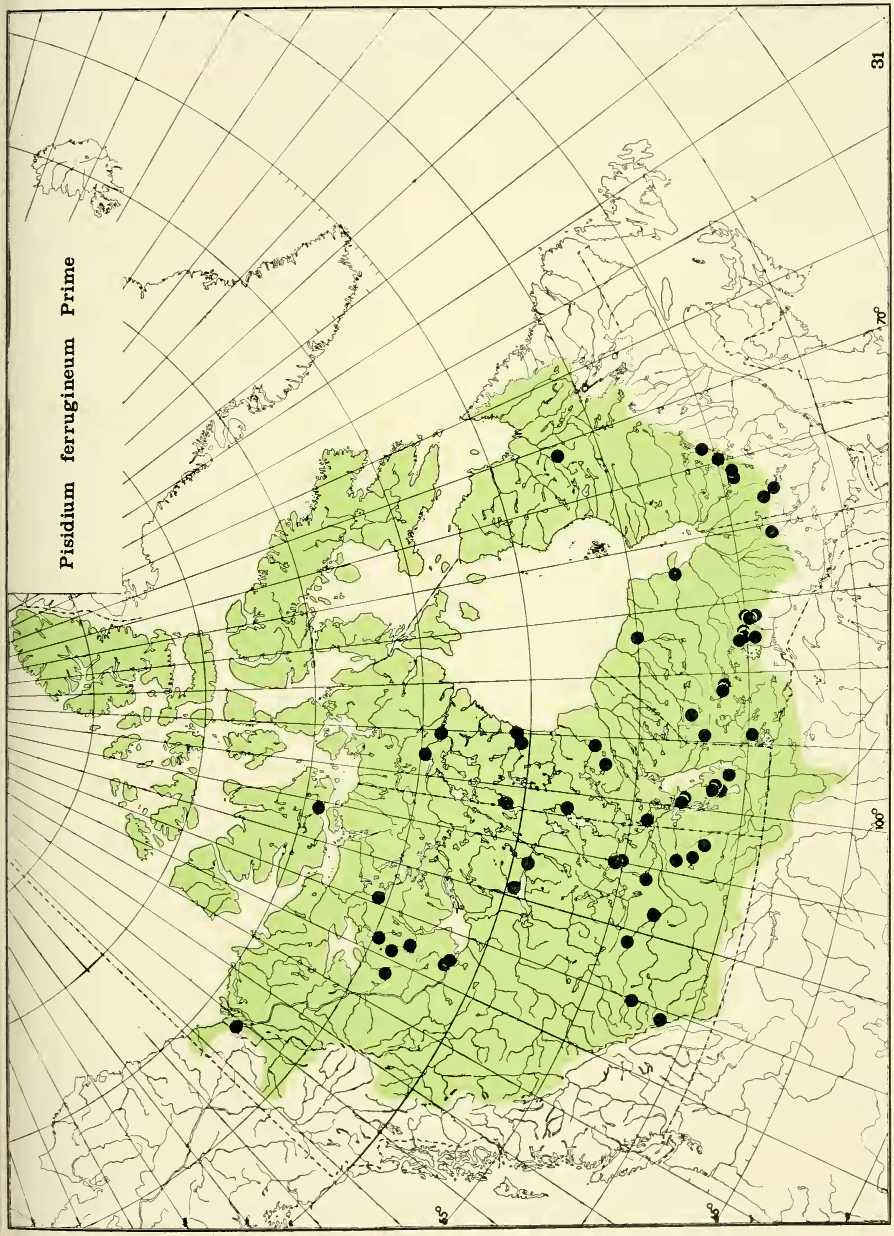
According to Herrington (1962: 40): "*ferrugineum* has a preference for cool climates. When found on a sandy bottom the striae are prominent and the beaks more or less tubercular. Those specimens obtained from lakes that are filling up with marl or developing a mucky bottom are smoother, have a greater diameter, and the beaks do not have the tubercular appearance. The varieties are much more common than the typical [=nominate] form with its strange tubercular beaks. Found in lakes, creeks, and rivers."

The only description of the soft parts of this species is a very inadequate one by Prime (1852: 362), viz.: "Foot very long and narrow, issuing from the anterior extremity of the shell. Siphons extremely short."

Pisidium (*Cyclocalyx*) *lilljeborgi* Clessin
Plate 18, Fig. 4; Map 32

Pisidium lilljeborgi Clessin (*in* Esmark & Hoyer), 1886: *Malak. Blätt.*, *8*(N.F.): 119. Type locality: "zuerst in Osterdalen [Norway] gefunden ist" [found first in Osterdalen].

P[*isidium*] *lilljeborgi* Clessin form *cristatum* Sterki, 1928: *Nautilus*, *42*(1): 25. Type locality not specified.


Pisidium ferrugineum Prime
31
70°
100°

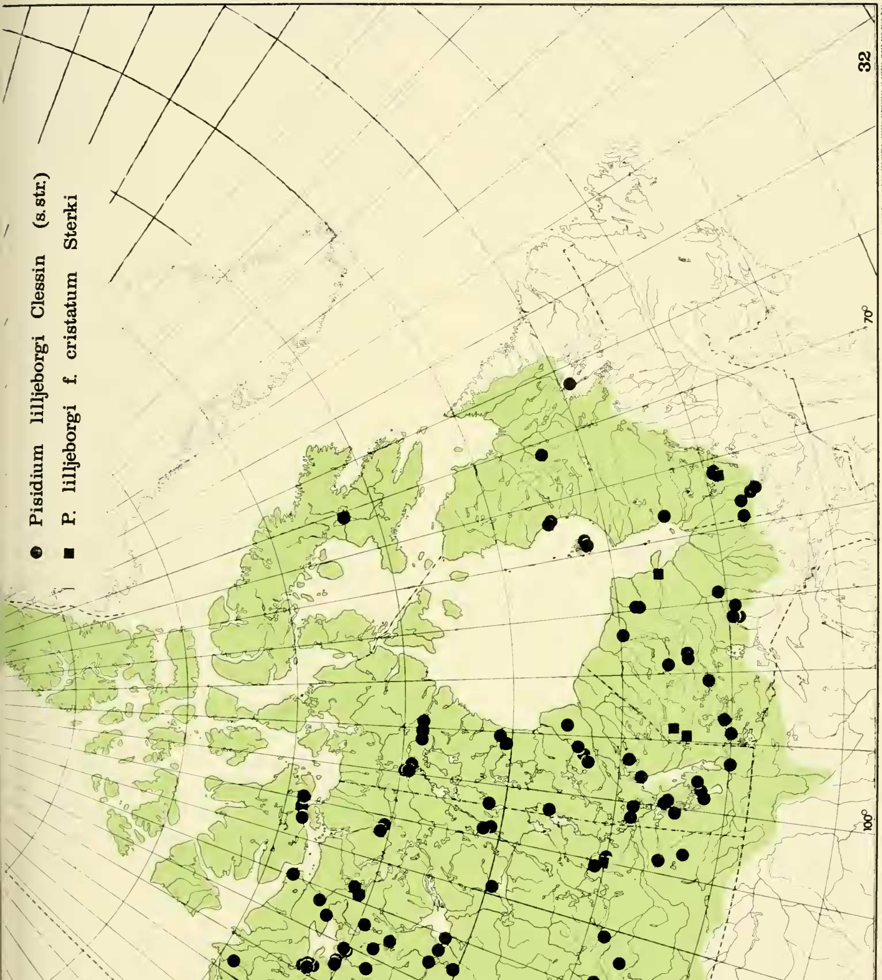
Diagnosis: Shell up to about $\frac{1}{6}$ inch long, subtriangular, relatively thin and inflated, and with umbones prominent and located posterio-dorsally. Western specimens are close to *Pisidium subtruncatum* but the anterior slope is shorter and more curved, the left cardinals are less alike, and the cusp of A1 is less proximal.

Description: " Shell short, moderately large, walls thin, usually considerably inflated, asymmetrical; beaks very prominent, fairly far back, broad and full, but more upright and blending into the shell than is the case with *Pisidium subtruncatum*; striae ranging from moderately fine to rather coarse; periostracum slightly dull to moderately glossy; dorsal margin very short, far back, openly curved and usually joining the ends with angles; posterior end roundly truncate, vertical, and joining ventral margin imperceptibly; anterior end a very long, somewhat rounded slope, joining ventral margin low with a more or less rounded angle; ventral margin long, well curved and swinging up at the posterior end where it passes into the dorsal margin (in many specimens the posterior end and the back part of the ventral margin make the segment of a circle); hinge short, openly curved; hinge-plate moderately heavy; laterals A1, A2 and P2 moderately long (A1 and A3 form a V); cusp of A1 proximal or on proximal side of center, or central (somewhat blunt on top), of A2 proximal (high and sharp on top); cardinals close to anterior cusps; C3 rather long, usually bent with anterior end parallel with hinge-plate, posterior end quite expanded; C2 short and broad; C4 narrow, twice or more as long as C2, beginning outside and extending straight (or in a gentle curve) back diagonally along hinge-plate to below its center, placing the posterior end of C2 and C4 quite a distance apart... "

" The form *P. lilljeborgi cristatum* differs from the type in having ridges on the beaks; the shell is usually shorter. " (Herrington 1962: 43-4).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Lac La Motte, 25 mi NW of Val d'Or, Que.					
1	3·6	3·3	0·92	2·3	0·64
5	3·5	3·0	0·86	2·3	0·66
9	3·4	2·8	0·82	2·2	0·65
13	3·0	2·7	0·93	2·0	0·67
Owl Lake, Man. (56°22′N, 94°55′W).					
1	3·5	3·3	0·94	2·5	0·71
5	3·4	3·2	0·94	2·4	0·71
9	3·3	3·0	0·91	2·4	0·73
13	2·9	2·6	0·90	2·1	0·73
Keith Arm, Great Bear Lake, N.W.T.					
1	4·0	3·5	0·88	2·7	0·68
5	3·8	3·4	0·90	2·5	0·66
9	3·6	3·1	0·86	2·4	0·67
13	3·4	2·8	0·82	2·0	0·59


● Pisidium lilljeborgi Clessin (s. str.)
■ P. lilljeborgi f. cristatum Sterki
32
70°
100°
55°
45°

Records:

More than 130 lots of *Pisidium lilljeborgi* (*s. str.*) are available so only marginal records are cited. *P. lilljeborgi* form *cristatum* was collected in only five localities and each of these is listed. See Map 32.

Pisidium lilljeborgi (*s. str.*)

Quebec. Lac Aigneau (57°10′N, 70°35′W) (1955, D. R. Oliver!). Waswanipi River, 22 mi NE of Demaraisville (this survey).
Ontario. Attawapiskat River, 6 mi W of Attawapiskat. Lake at source of Shell Brook (55°20′N, 87°17′W) (both this survey).
Manitoba. Pond 6 mi W of Whitemouth. Owl Lake (57°22′N, 94°33′W). Reindeer Lake, Brochet (all this survey).
Saskatchewan. Echo Lake, Qu'Appelle River Valley (1964, D. L. Delorme!). Camsell Portage, Lake Athabasca (1945, D. S. Rawson!).
Alberta. Bullpound Lake, 4½ mi S of Hanna. Peace River just below Point Providence (1921, E. J. Whittaker!). Jasper National Park (3 localities) (1954, Can. Wildlife Serv.!).
Northwest Territories. Nettilling Lake, Baffin Island (1957, D. R. Oliver!). Keyhole Lake, Victoria Island (69°23′N, 106°14′W) (1962, Fish. Res. Bd.!). Greiner Lake, Victoria Island (69°12′N, 104°55′W). Dismal Lake (67°14′N, 116°33′W) (both 1959 Fish. Res. Bd.!). Mackenzie River, Aklavik (1957, Fish. Res. Bd.!).

Pisidium lilljeborgi form *cristatum*

O'Sullivan River, ½ mi N of Miquelon, Que. Attawapiskat River, 6 mi W of Attawapiskat, Ont. Deer Lake, Deer Lake, Ont. Stout Lake, Ont., at outlet (52°08′N, 94°44′W) (all this survey). Lac la Ronge, Sask., from whitefish (date ?, Univ. Sask.!).

Distribution: Southern Baffin Island west (south of 70°N) to Alaska and the Aleutian Islands, south throughout Canada to New England and the northern tier of states, and farther south in the Rocky Mountains to Colorado, Utah, and California. Also, Iceland and northern Europe.

Biology and Ecology: The 34 population samples collected during this survey are from the following habitats: 22 are from large lakes, 3 from small lakes, 1 from a pond (area ½ acre), 5 are from streams of various widths from about 400 feet to 20 feet, and 3 are from narrow, slow-moving side channels or backwaters of large rivers. Vegetation was present at 27 localities and medium to sparse at 24. Bottom deposits were variable with sand occurring slightly more frequently. In the 5 lotic localities current was recorded as moderate, slow or imperceptible.

Pisidium lilljeborgi occurs in " lakes and rivers, with a preference for lakes; found in fine sand containing scattered small weeds " according to Herrington (1962 : 44). Ecological data from this survey corroborate his statement, but the substrata inhabited include mud, clay, and gravel as well as sand.

Odhner (1929: 61) has discussed the anatomy, reproduction, and ecology of this species in Sweden. Young are found from June to September and up to 13 occurred in a single individual. The length of that adult was 3·7 mm and the young varied from 1·0 to 1·1 mm long.

Remarks: Except for the Quebec locality, the *cristatum* morph of *Pisidium lilljeborgi* was found in company with the typical morph in all localities recorded above. Although the collections of *cristatum* are all from the Precambrian Shield or from the edge of the Shield (Lac la Ronge) and presumably from soft water, farther south the morph also occurs in hard water.

Pisidium (*Cyclocalyx*) *milium* Held
Plate 18, Fig. 5; Map 33.

Pisidium milium Held, 1836: *Isis von Oken*. Heft *4*: 282. Type locality: " in der nähern Umgegend Münchens " [in the vicinity of Munich, Germany].

Diagnosis: Shell up to about ⅛ inch long, thin, inflated, subtriangular, truncated posteriorly and (in end view) truncated ventrally. Close to *Pisidium nitidum*

but less high, with ventral margin less curved, and anterior cusps less distal and sharper.

Description: " Shell small, long; walls thin, much inflated; beaks rather far back, considerably swollen and prominent; periostracum very glossy; striae rather widely spaced, but frequently low; " rest periods " quite prominent; dorsal and ventral margins parallel; dorsal margin short and considerably curved; ventral margin long and almost straight; posterior end truncate or rounded, almost vertical, and at right angles to both dorsal and ventral margins; anterior end a long, rather steep slope descending very low to where it joins the ventral margin with a sharp angle; hinge-plate narrow and not very long; laterals rather short; cusps inclined to be sharp on top; cusps of left valve toothpick-like, of A1 and A2 central or on distal side of centre, of P2 somewhat distal; cardinals fairly near anterior cusps, but varying, sometimes subcentral; C3 slightly curved and uniform in width; C2 and C4 nearly same thickness and about parallel; C4, begins well over C2, slightly curving or straight (C2 is the shorter of the two).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Small lake, 3 mi N of Geraldton, Ont.					
1	3·0	2·5	0·83	2·4	0·80
3	2·5	1·9	0·76	1·9	0·76
5	2·4	1·8	0·75	1·7	0·71
7	2·1	1·6	0·76	1·3	0·62
Pelican Lake, Sioux Lookout, Ont.					
1	2·6	2·2	0·85	1·9	0·73
2	2·4	1·9	0·79	2·0	0·83
3	2·3	1·9	0·83	2·0	0·87
4	2·2	1·9	0·86	2·1	0·95
Hector Lake, 10 mi NNW of Lake Louise, Alta.					
1	2·5	2·2	0·88	1·5	0·60
5	2·4	1·9	0·79	1·7	0·71
9	2·3	1·9	0·83	1·7	0·74
13	2·2	1·8	0·62	1·5	0·68

Records:

Ontario. Lillabelle Lake, 4 mi N of Cochrane. Abitibi River, 17 mi N of Cochrane. Monument Channel at portage, 20 mi W of Attawapiskat. Klotz Lake, 30 mi E of Longlac. Small lake 3 mi N of Geraldton. Hutchinson Lake, 5 mi N of Geraldton (all this survey). Head of Lake St. Joseph (1905, W. McInnes!). McCaulay Creek, 15 mi W of Atikokan. Pelican Lake, Sioux Lookout. Bamaji Lake (51°10′N, 91°25′W) (all this survey).

Manitoba. Two lots labelled " Manitoba " collected by Robert Bell in 1906.

Saskatchewan. Halkett Lake, 20 mi S of Waskesiu (this survey). Lac la Ronge, from whitefish (1954, Univ. Sask.!). Kipabiskau Lake (52°34′N, 104°09′W) (date, collector?).

Alberta. Caché Lake, 2 mi W of Spedden. Whitney Lake, 6 mi SE of Lindbergh. Tawatinaw River, 1 mi N of Rochester. Third Vermilion Lake, Banff. Hector Lake, 10 mi NNW of Lake Louise (all this survey). Edith Lake, Jasper National Park (Can. Wildlife Serv.!).

Northwest Territories. Lac la Martre (63°10′N, 117°20′W) (1959, Fish. Res. Bd.!).

PLATE 18. *Pisidium* (II)

FIG. 1. *Pisidium equilaterale*, Ottawa River near Mattawa, Ontario (NMC 19090, 3·0 mm), . . p 177.

FIG. 2. *Pisidium fallax*, Knee Lake, northern Manitoba (NMC 1925, 3·5 mm), ... p 179.

FIG. 3. *Pisidium ferrugineum*, Lac la Ronge, Saskatchewan (NMC 19013, 2·4 mm), ... p 181.

FIG. 4. *Pisidium lilljeborgi*, Lac la Ronge, Saskatchewan (NMC 19004, 3·3 mm), ... p 182.

FIG. 5. *Pisidium milium*, Klotz Lake, near Longlac, Ontario (NMC 19135, 2·5 mm), ... p 186.

FIG. 6. *Pisidium nitidum* (*s. str.*), Klotz Lake, near Longlac, Ontario (NMC 15573, 2·4 mm), . p 190.

FIG. 7. *Pisidium nitidum* (*pauperculum* morph), Rice Lake, Otonobee Township, Ontario (NMC 3981, 2·6 mm), ... p 191.

FIG. 8. *Pisidium nitidum*(*contortum* morph), Beachburg, Ontario (NMC 6525, 2·7 mm), ... p 191.

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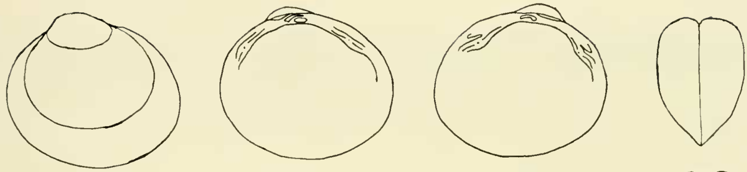

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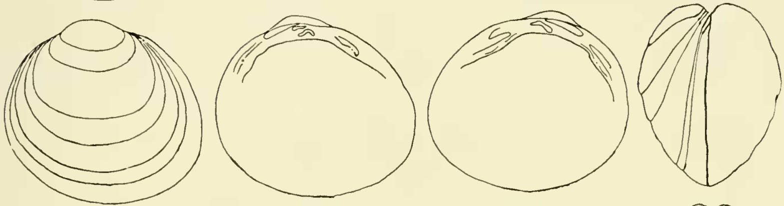

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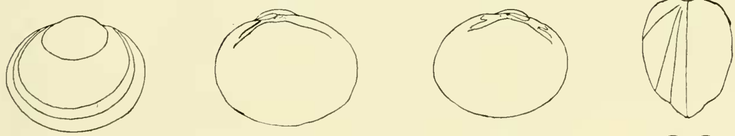

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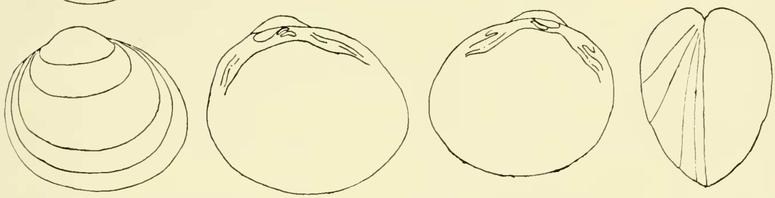

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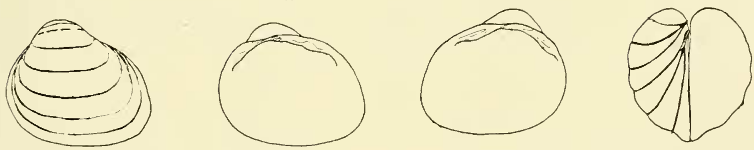

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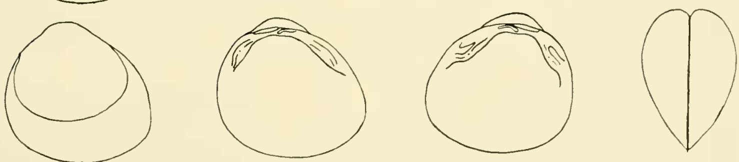

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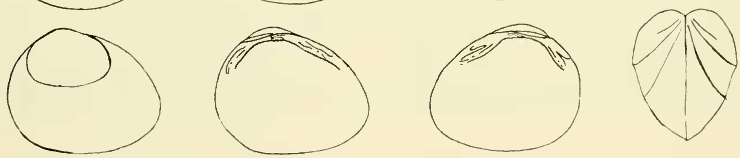
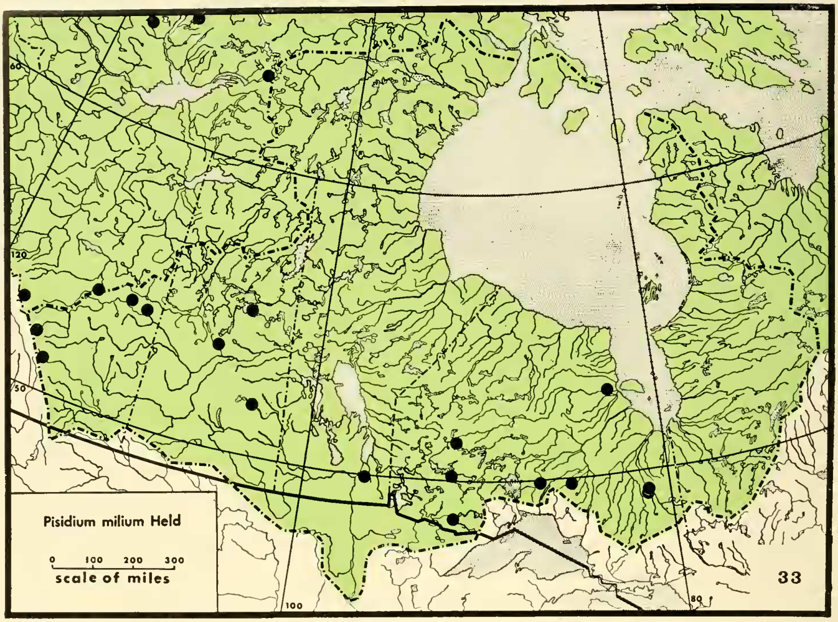




Distribution: Prince Edward Island; New Brunswick and Maine northwest to the vicinity of James Bay and beyond to north of Great Slave Lake and to the Aleutian Islands, west to British Columbia and Montana, and south in the Rocky Mountains to Utah and Colorado. Also Europe.

Biology and Ecology: The 16 lots of *Pisidium milium* collected during this survey are from the following habitats: 6 are from large lakes, 3 from small lakes, and 7 are from rivers and streams of various widths from about 500 feet (Abitibi River, Ont.) to 25 feet (Inlet of Third Vermilion Lake, Alta.). Aquatic vegetation and muddy bottom occurred wherever *P. milium* was found alive. Current in stream habitats was moderate, slow, or (in one instance) not perceptible.

Herrington (1962: 45) gives: " Mud and ooze bottom in creeks and rivers, but mostly in ponds and small lakes... rather scarce and only a few in a habitat. "

Odhner (1929: 91) has described the anatomy of *Pisidium milium* from Sweden and has commented on its reproduction and ecology. One specimen 2·2 mm long was kept isolated in the laboratory for ten months and then produced young, 0·9 mm long, presumably through self-fertilization. No such studies of North American populations have been made.

Pisidium (*Cyclocalyx*) *nitidum* Jenyns
Plate 18, Figs. 6-8; Map 34.

Pisidium nitidum Jenyns, 1832: *Trans. Cambridge phil. Soc.*, *4*: 304, pl. 20: 7, 8. Type locality: " widely dispersed throughout Cambridgeshire . . . [and] in the ditches about Battersea Fields, and in other parts of Surrey [England]."

Pisidium contortum Prime, 1854: *Ann. Lyceum natr. Hist. New York*, *6*: 65, pl. 1: 2a-c. Type locality: "found subfossil at Pittsfield, Mass."
Pisidium pauperculum Sterki, 1896: *Nautilus 10*: 64. Type locality not specified (14 localities mentioned distributed from Massachusetts to New Jersey and Wisconsin).

Diagnosis: *Pisidium nitidum* (*s.str.*): Shell up to about ⅛ inch long, ovate-rhomboid, rather thin, with low, subcentral umbones and glossy periostracum. Like *P. milium* but higher, with ventral margin more curved and anterior cusps more distal and not as sharp.

Description : *Pisidium nitidum* (*s. str.*): "Shell moderately small, walls thin, rhomboid, of small diameter; beaks subcentral, broad, not very prominent; periostracum glossy; striae moderately fine, uniform and distinct (in some lots quite prominent), heavy striae around beaks not as common in North American specimens as in European; dorsal margin long, evenly curved, joins ends without angle; ventral margin more gently curved; anterior end with a rounded slope joining ventral margin low in a rounded point; posterior end vertical or undercut, joining ventral margin imperceptibly; hinge long, of moderate width and somewhat curved; laterals of moderate length, straight or flaring outward at distal end; cusps rather prominent, but inclined to be blunt on top; cusp of A1 distal or on distal side of centre, of P1, P2 and A2 rather distal; cardinals subcentral; C3 gently curved, of uniform width except at posterior end, and almost parallel with hinge-plate; C2 slightly heavier than C4; C4 straight or gently curved, about parallel with C2; space between the 2 of uniform width, straight or a little curved, and usually directed across hinge-plate at a gentle angle. The cardinals of *P. nitidum* are much as in *P. subtruncatum* but shorter." (Herrington, 1962: 45).

Pisidium nitidum form *contortum* is much more elongate, with a nearly straight ventral margin, and with the anterior end produced and roundly pointed basally. (See Pl. 18, Fig. 8).

Pisidium nitidum form *pauperculum* is rather short, heavy, high, with dorsal margin more curved and with cardinal teeth more nearly central than in *P. nitidum* (*s. str.*). (See Pl. 18, Fig. 7).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Beaverlodge Lake, N.W.T. (64°39′N, 118°08′W) (*P. nitidum s. str.*).					
1	2·5	2·0	0·80	1·6	0·64
5	2·4	2·0	0·83	1·5	0·62
9	2·2	2·0	0·91	1·3	0·59
13	2·0	1·7	0·85	1·2	0·60
Klotz Lake, 30 mi E of Longlac, Ont. (*P. nitidum* form *contorum*).					
1	2·5	2·0	0·80	1·5	0·60
2	2·4	1·8	0·75	1·6	0·67
3	2·3	1·7	0·74	1·8	0·78
4	1·8	1·5	0·83	1·2	0·67
Denbeigh Point, Lake Winnipegosis, Man. (*P. nitidum* form *pauperculum*).					
1	2·5	2·3	0·92	1·7	0·68
5	2·4	2·3	0·96	1·5	0·62
9	2·2	1·9	0·86	1·3	0·59
13	2·0	1·7	0·85	1·2	0·60

Records:

About 100 lots of *Pisidium nitidum* (*s. str.*), 35 lots of *P. nitidum* form *pauperculum*, and 4 lots of *P. nitidum* form *contortum* are available from the research area. Only marginal records and appropriate notes are given for the first two morphs but all localities for the *contortum* morph are cited. See Map 34.

Quebec. *P. nitidum* (*s. str.*): Lac Aigneau (57°10′N, 70°35′W) (1955, D. R. Oliver!). Lake Chibougamau, southwest arm, 15 mi S of Chibougamau. Lac Dubuisson, 4 mi NW of Val d'Or (both this survey).

Ontario. *P. nitidum* (*s. str.*): Abitibi River 17 mi N of Cochrane. Winisk River, 15 mi S of Winisk (both this survey). *P. nitidum* form *contortum*: Nellie Lake, 27 mi S of Cochrane. Klotz Lake, 30 mi E of Longlac. Lydia Lake, 23 mi E of Longlac. Two Mile Lake, 3 mi S of Nakina (all this survey). *P. nitidum* form *pauperculum*: Unnamed lake, source of Shell Brook (55°20′N, 87°17′W) (the only Ontario record from the Hudson Bay drainage area; this survey).

United States. *P. nitidum* (*s. str.*): Traverse Lake, Brown's Valley, Minn. Lake 11 mi W of St. John, N.D. (both this survey). *P. nitidum* form *pauperculum*: Traverse Lake, Brown's Valley, Minn. (this survey).

Manitoba. *P. nitidum* (*s. str.*): Falcon Lake, (49°41′N, 95°15′W). Owl Lake (57°22′N, 94°33′W). Reindeer Lake, Brochet (all this survey). *P. nitidum* form *pauperculum*: Goose Lake, Roblin (this survey). Denbeigh Point, northwest extremity of Lake Winnipegosis (1964, M. Ouellet!).

Saskatchewan. *P. nitidum* (*s. str.*) and *P. nitidum* form *pauperculum*: Whitesand River, 9 mi ENE of Sheho. Waden Bay, Lac la Ronge (both this survey).

Alberta. *P. nitidum* (*s. str.*): Third Vermilion Lake, Banff (this survey). "The Willows", Lake Athabasca (1945, D. S. Rawson!). *P. nitidum* form *pauperculum*: Third Vermilion Lake, Banff. Driftwood River, 2½ mi N of Spurfield (both this survey).

Northwest Territories. *P. nitidum* (*s. str.*): Bernard Harbour (1915, F. Johansen!). Aklavik (1957, Fish. Res. Bd.!).

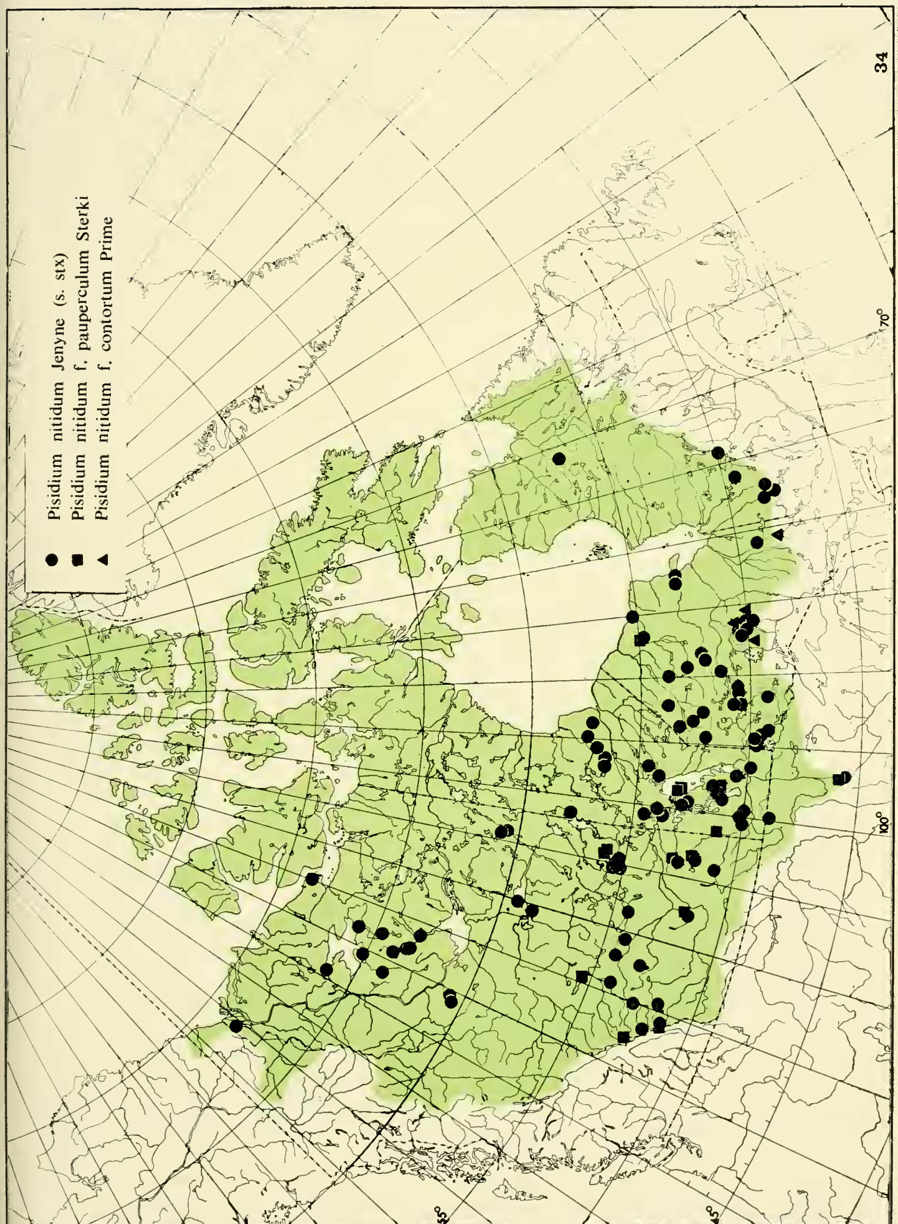
Distribution: Herrington (1962: 47) states that *Pisidium nitidum* (*s. lato*) occurs in all Canadian provinces (except Nova Scotia) and the Northwest Territories, in most parts of continental United States (except Alaska), and in Mexico, Eurasia, and Egypt. Baker (1928b) gives the range of "*Pisidium contortum*" as Maine, Ontario, Michigan, Massachusetts, and Wisconsin and of "*Pisidium pauperculum*" as New England and New York to Ohio, Ontario, and Minnesota.

Biology and Ecology: The 51 lots of *Pisidium nitidum* (*s. str.*) collected during this survey are from the following habitats: 22 are from large lakes, 10 from small lakes, 3 from permanent ponds, and 16 from rivers and streams of diverse widths from over 400 feet down to about 10 feet. Vegetation varied in abundance from sparse to thick and was absent at only 3 localities. Bottom deposits were also diverse but mud was present at most (38) of the habitats. Current in lotic environments was moderately slow or imperceptible.

The 12 lots of *Pisidium nitidum* form *pauperculum* are from 9 large lakes, 2 small lakes, and 1 large (200 feet wide), shallow (2 feet deep), rather swift-flowing river. Vegetation was of variable abundance but was absent at 4 localities. Bottom deposits were partly or wholly of mud at all stations.

The 4 lots of *Pisidium nitidum* form *contortum* are from 1 large lake and 3 small lakes. All lots except 1 (a single specimen) were found associated with *P. nitidum* (*s. str.*). Vegetation was thick at 3 localities and sparse at one. Bottom deposits were of mud at 2 localities, sand and mud at 1, and sand and clay at 1.

Herrington (1962: 46) gives the habitat of this species as "Large ponds, bog ponds, lakes, creeks and rivers. Seems to prefer shallow water; fairly common." The data from this survey are in agreement with this and extend the statement to include large lakes. No physical ecological differences bet-


Pisidium nitidum Jenyne (s. stx)
Pisidium nitidum f. pauperculum Sterki
Pisidium nitidum f. contortum Prime
34
70°
100°
55°
45°

ween the three " forms " are evident (see " Remarks " below).

The anatomy and reproduction of *Pisidium nitidum* has been described by Odhner (1929: 81). Partly-grown specimens of 1·4 and 1·5 mm long, presumably born only 1 month earlier, contained 2 embryos. In larger specimens the number of embryos was found to vary from 2 to 7 and they were held in the gills of the parent all summer. The largest specimens (3 mm long) were without young.

Remarks: The distribution of the forms *pauperculum* and *contortum* in the Canadian Interior Basin appears to be ecologically and taxonomically significant. See Map 34.

The *pauperculum* morph has not been found in the lime-poor waters of the Precambrian Shield. Since it is differentiated from *Pisidium nitidum* (*s. str.*) principally in that it is more heavily calcified, it may be restricted to hard water. Present data are insufficient to judge its taxonomic status, but it occurs in mixed lots with *P. nitidum* (*s. str.*) and may prove to be a separate species.

Living populations of the *contortum* morph are restricted, in the Canadian Interior Basin, to central Ontario. Fossils (probably Pleistocene) of this morph are known from Lady Lake, Saskatchewan and from the Peace River, Alberta, just below Point Providence. The present circumscribed range of the morph, and the previous wide range (including regions outside the Precambrian Shield) are indications that it may be a distinct species. Clearly the status of both morphs requires further study.

Pisidium (*Cyclocalyx*) *subtruncatum* Malm
Plate 19, Fig. 1; Map 35.

Pisidium subtruncatum Malm, 1855: *Götheborgs Kongliga Vetenskaps och Vitterhets Samhallet Handlingar*, *3*: 92, text figs. Type locality: " Sweden."

Diagnosis: Shell up to slightly more than $\frac{1}{8}$ inch long, of medium thickness, ovate, much inflated, glossy, and with umbones prominent and posterio-dorsal. Like *Pisidium walkeri*, but more inflated, with the cusp of A1 more proximal and with left cardinals parallel. Also rather like *P. lilljeborgi*, which see for comparison.

Description: " Shell varying in size from rather small to medium; walls thin; long to rather short; periostracum usually glossy; striae moderately fine and evenly spaced; beaks narrow, prominent and far back, tilted back and not blending quickly into body of shell; dorsal margin short, not parallel with ventral margin but far back, joining anterior end above, or at, anterior cusps with an angle, also joining posterior end with angle; anterior end usually long (but in short specimens it is short and steep) with long, almost straight slope, beginning above or at anterior cusps and joining ventral margin in low rounded point; posterior end roundly truncate, passing into ventral margin without angle; ventral margin gently rounded; hinge short and openly rounded; hinge-plate narrow; laterals rather long, cusps prominent; cusps of A1 and A2 proximal to central, of P1 and P2 central; cardinals near anterior cusps or subcentral; C2 and C4 roughly parallel, posterior ends slightly nearer inner edge of hinge-plate; C3 long and not much curved; width of hinge-plate and size of shell influences cardinals considerably.

A North American form of *Pisidium subtruncatum* in the western part of the United States and in Canada north to Great Slave Lake, Northwest Territories (which I have been calling a " western form"), has considerable resemblance to *P. lilljeborgi.* " (Herrington, 1962: 48).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Abitibi River, 17 mi N of Cochrane, Ont.					
1	3·8	3·1	0·82	2·8	0·74
5	3·2	3·0	0·94	2·2	0·69
9	2·9	2·5	0·86	2·1	0·72
13	2·7	2·3	0·85	2·0	0·74
Lac la Ronge, Sask.					
1	3·5	3·0	0·86	2·3	0·66
5	2·9	2·3	0·79	1·6	0·55
9	2·7	2·0	0·74	1·6	0·59
13	2·6	2·1	0·81	1·4	0·54
Mills Lake, N.W.T. (61°30′N, 118°20′W).					
1	3·2	2·9	0·91	2·1	0·66
3	3·1	2·8	0·90	2·1	0·68
5	3·0	2·7	0·90	2·0	0·67
7	2·8	2·5	0·89	1·8	0·64

Records:

Since approximately 60 lots are available from the research area only marginal records are cited. See Map 35.

Quebec. Small river 9 mi NE of Demaraisville. Lac La Motte, 25 mi NW of Val d'Or (both this survey).

Ontario. Albany River near Fort Albany (3 localities). Attawapiskat River near Attawapiskat (3 localities). Winisk River near Winisk (2 localities). Unnamed lake, source of Shell Brook (55°20′N, 87°17′W) (all this survey).

Manitoba. Pond 6 mi W of Whitemouth. Owl, Lake (56°22′N, 94°35′W). Reindeer Lake Brochet (all this survey).

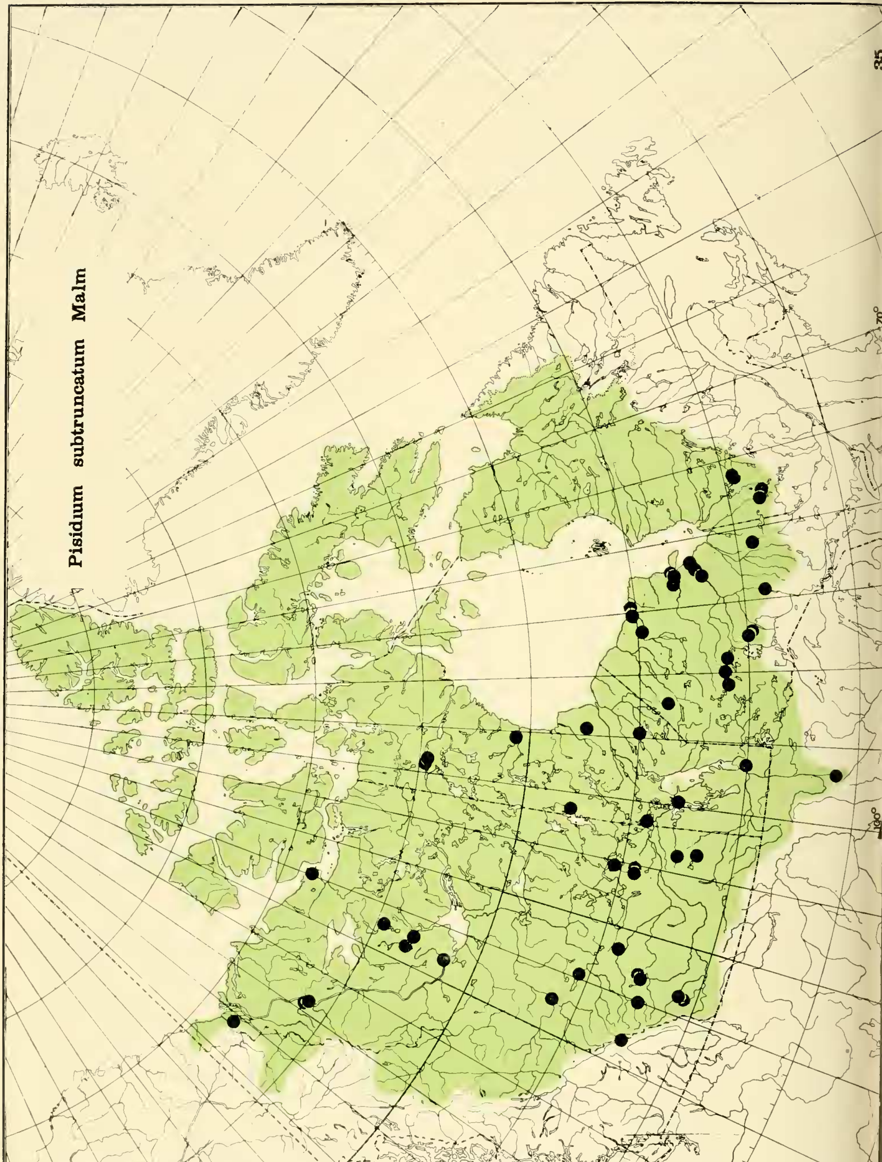
Minnesota. Traverse Lake, Brown's Valley (this survey).

Saskatchewan. Whitesand River, Sheho (this survey). Lac la Ronge (5 lots, mostly from whitefish) (1950–54, Univ. Sask.!).

Alberta. Gull Lake, 7 mi W of Lacombe. Driftwood River, 2½ mi N of Spurfield (both this survey). Pyramid Lake, Jasper National Park (1954, Can. Wildlife Serv.!).

Northwest Territories. Hyde Lake (60°45′N, 95°22′W) (1959, Fish. Res. Bd.!). Aberdeen Lake (64°45′N, 100°00′W) (1961, Elizabeth Macpherson!). Lake at Bernard Harbour (68°45′N, 114°45′W) (1916, Can. Arctic Exped.!). Aklavik (1957, Fish. Res. Bd.!).

Distribution: In Canada from central Quebec northwest near the west side of James Bay and Hudson Bay and beyond to Coronation Gulf and the Mackenzie River estuary (see Map 35); also west to British Columbia. In the


Pisidium subtruncatum Malm
35
70°
100°
55°
45°

United States from New York to Montana and south in the Rocky Mountains to Colorado and California. Also in Europe.

Biology and Ecology: The 34 lots of *Pisidium subtruncatum* collected during this survey are from the following habitats: 14 are from large lakes, 3 from small lakes, 1 from a permanent pond (area about ½ acre), 15 from rivers and streams of various widths from about 400 to about 10 feet, and 1 from a muskeg pool. Vegetation varied in density but was present at all localities, and substrates were of all kinds with mud slightly the more frequent. Current velocity in rivers and streams varied from rapid to imperceptible, with moderate or slow currents most frequently met.

Under " Habitat " Herrington (1962: 49) states: " Streams, bays, and lakes, including the Great Lakes. In Europe they are abundant, but on this continent there are only a few at a station. The ' western form ' is very abundant where found. " Present data extend this summary to include ponds and muskeg pools. In addition, the densest population seen (225 specimens collected) was in the east, at Abitibi River 17 mi N of Cochrane, Ont., a wide (400-foot), moderately-flowing, deep, muddy river. There, 8 other *Pisidium* species occured with *P. subtruncatum* but the latter was more abundant than all the others combined.

The anatomy of this species has been discussed and figured by Odhner (1929: 74). Two small litters are born each year in Swedish populations (Odhner, loc. cit.) and individual life spans exceed 1 year (Heard, 1965: 406).

Pisidium (*Cyclocalyx*) *variabile* Prime
Plate 19, Fig. 2; Map 36.

Pisidium variabile Prime, 1852: *Proc. Boston Soc. natr. Hist.*, *4*: 163. Type locality: " Fresh Pond [Cambridge, Mass.] and its environs."

Diagnosis: Shell up to nearly 1/5 inch long, rather thick-walled, triangular-ovate and variable, inflated, surface glossy, hinge-teeth heavy, and umbones prominent, broad, and located posterio-dorsally. Like some specimens of *Pisidium equilaterale*, *P. casertanum*, *P. compressum*, and *P. nitidum* form *pauperculum* (compare).

Description: " Shell heavy, varying from short and high to moderately long; beaks rather prominent, quite far back and broad; striae rather coarse to rather fine; periostracum glossy; dorsal margin short and round; anterior end begins near beaks without angle, has a rather steep, almost straight slope which begins near the proximal side of cusps and descends to where it joins ventral margin with an angle; ventral margin long (in the longer specimens three times that of the dorsal margin) and considerably curved, passing into posterior end without angle; posterior end broadly rounded, vertical or slightly undercut; hinge long, heavy and rather steeply curved; laterals rather short. incorporated into hinge-plate; A3 and P3 tend to curve around pit of sulcus; cusps blunt on top; cusps of A1 distal, of P1, A2 and P2 central or on distal side of center; cardinal central; C3 short, much curved, posterior end much the larger; C2 short and stout like an inverted D; C4 fairly short, only slightly curved and directed toward cusp of P2; considerable space between posterior ends of C2 and C4." (Herrington, 1962: 50).

Herrington (pers. comm. Oct. 24, 1968) has commented further as follows: " The hinge characters of *P. variabile* and *P. compressum* are practically identical. This is true of no other species of *Pisidium.* "

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Opasitika Creek tributary, 21 mi W of Kapuskasing, Ont.					
1	4·7	4·2	0·89	2·9	0·62
5	4·3	3·7	0·86	2·8	0·65
9	4·1	3·4	0·83	2·4	0·59
13	3·6	3·0	0·83	2·0	0·56
Second Vermilion Lake, Banff, Alta.					
1	4·7	4·1	0·87	2·8	0·60
5	3·7	3·2	0·87	2·4	0·65
9	3·4	3·3	0·97	2·3	0·68
13	3·2	3·1	0·97	2·2	0·69
Wholdaia Lake, N.W.T. (60°45′N, 104°30′W).					
1	3·7	3·0	0·81	2·2	0·59
3	3·5	2·7	0·77	1·9	0·54
5	3·3	2·8	0·85	2·0	0·61
7	3·2	2·3	0·72	1·8	0·56

Records:

Since over 135 lots are available, only marginal records are cited. See Map 36.

Quebec. Lac Aigneau (57°10′N, 70°35′W) and nearby pond (both 1955, D. R. Oliver!). Bordeleau River, 20 mi NE of Chibougamau. Bell River, 33 mi N of Senneterre. Lac Dubuisson, 4 mi NW of Val d'Or (all this survey).

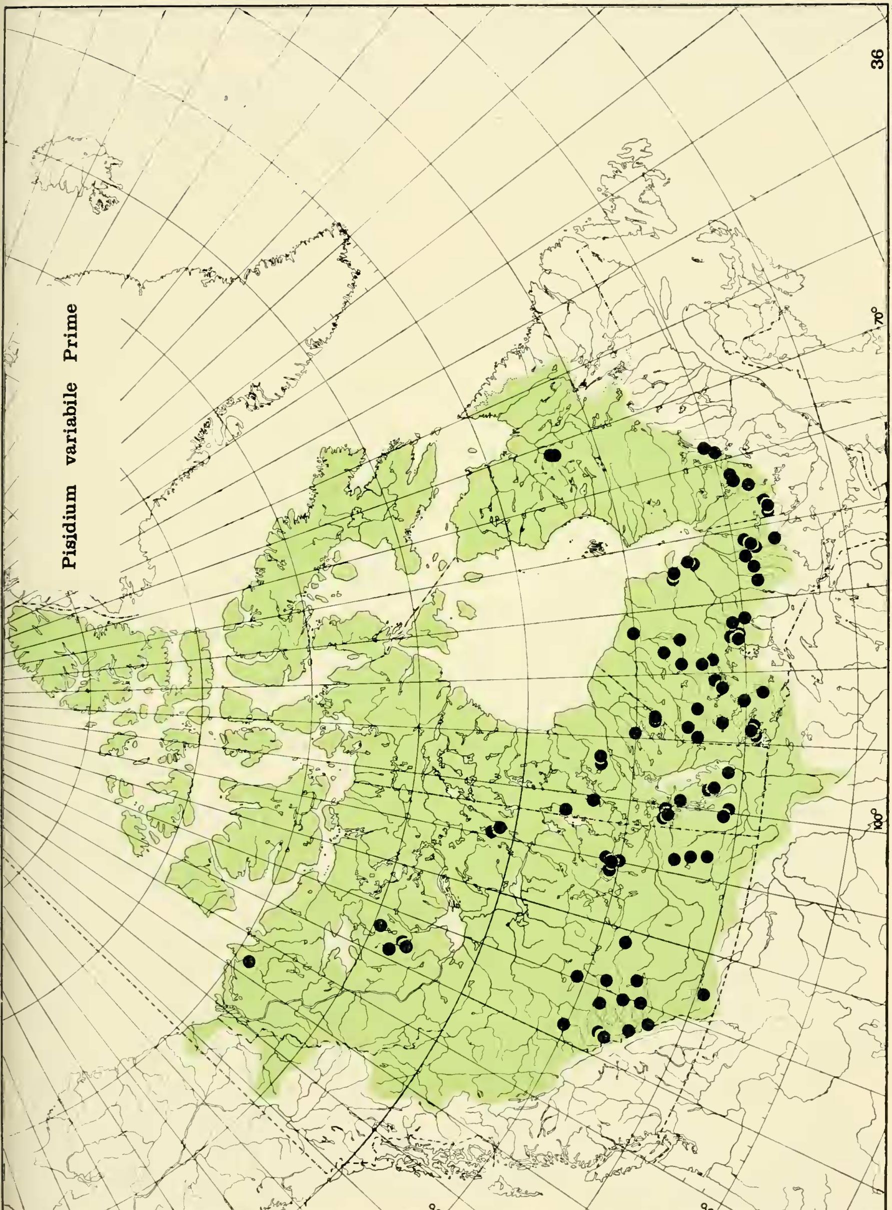
Ontario. St. Ann's Lake and Yellow Creek, both near Fort Albany. Attawapiskat River near Attawapiskat (2 localities). Unnamed lake, source of Shell Brook (55°20′N, 87°17′W) (all this survey).

Manitoba. Minnedosa River, 11 mi NNE of Elphinstone. Red Sucker Lake (54°10′N. 93°36′W and 54°10′N, 93°57′W, 2 localities), Limestone Lake (56°35′N, 96°00′W) (all this survey).

North Dakota. Uppsilon Lake, Turtle Mountains (1920, C. T. & N. A. Wood!).

Saskatchewan. Whitesand River, 9 mi ESE of Sheho. Twin Lake, 35 mi N of La Ronge (both this survey). Lac la Ronge (numerous lots, this survey and Univ. Sask.!).

Alberta. Chin Lake, 13 mi E of Lethbridge. Second Vermilion Lake, Banff. Driftwood River, 2½ mi N of Spurfield. Clairmont Lake, 2 mi NE of Clairmont (all this survey).


Pisidium variabile Prime
36
70°
100°
55°
45°

Northwest Territories. Wholdaia Lake (60°45′N, 104°30′W). Lac la Martre (63°10′N, 117°20′W). Beaver Lodge Lake (64°39′N, 118°08′W). Anderson River (all 1958, 1959, Fish. Res. Bd.!).

Distribution: Nova Scotia and Prince Edward Island to Labrador (Astray Lake) and Ungava, northwest to near the Arctic Coast at Anderson River, west to British Columbia, and south throughout most (possibly all) of the United States.

Biology and Ecology: The 73 lots of *Pisidium variabile* collected during this survey are from the following habitats: 30 are from large lakes, 10 from small lakes, 2 from permanent ponds, and 31 from streams of various widths (200 feet to 8 feet). Vegetation was present at nearly all localities (thick to sparse), bottom sediments were various (principally mud), and current was discernible but variable (mostly slow) at all lotic habitats.

According to Herrington (1962: 50) this species occurs in " creeks, rivers, and lakes; usually in still water where soft sediments accumulate. " The above data corroborate this and add permanent ponds to the list of suitable habitats.

Heard (1965: 395) working with a Michigan population, states that gametogenesis occurred principally during late summer and early fall and that mature gametes occurred most abundantly during the winter. He also found (Heard, 1964: 48) that litter size ranged from 12 to 34 mm (average 27·8) in 8 specimens examined on June 3, 1961. No anatomical studies of *Pisidium variabile* have been published.

Pisidium (*Cyclocalyx*) *ventricosum* Prime
Plate 19, Figs. 3, 4; Map 37.

Pisidium ventricosum Prime, 1851: *Proc. Boston Soc. natr. Hist.*, *4*: 68. Type locality: " a small stream running out of Fresh Pond, Cambridge [Massachusetts]."

Pisidium rotundatum Prime, 1852: *Proc. Boston Soc. natr. Hist.*, *4*: 164. Type locality: " Lake Superior."

Diagnosis: Shell up to about $\frac{1}{8}$ inch long, inflated (some specimens are nearly globular), thin; with glossy periostracum and umbones prominent and posterio-dorsal. Resembles some specimens of *Pisidium ferrugineum* but in *P. ventricosum* the anterior end is not sloped, the hinge is shorter, and the cusp of A2 is proximal.

Description: (*Pisidium ventricosum* form *rotundatum*): " Shell very small, walls thin, more or less oval in outline, well inflated; striae moderate to very fine, evenly spaced; periostracum glossy; beaks rather prominent and well posterior; dorsal margin short and well rounded; ventral margin long and more openly rounded; posterior end well rounded and vertical; anterior end descending rather low, round, shell without an angle; hinge very short, far back but almost parallel with ventral margin; hinge-plate narrow; laterals short; cusps short and high with near-vertical ends; cusps of A2 proximal, of P2 and A1 central or on distal side of centre; cardinals close to anterior cusps; C3 curved, but not much enlarged at posterior end. . . ; C2 and C4 short; C2 almost parallel with hinge-plate, straight, sometimes slightly curved, or just a peg; C4 straight or slightly curved, sometimes parallel with hinge-plate, but more often directed slightly downward, then not parallel with C2; proximal end of posterior sulcus of right valve closed by a pseudocallus on inner side of proximal end of P3 and, therefore, does not run out on top of hinge-plate. "

" *P. ventricosum* (*s. str.*) has a heavy hinge. . .the beaks are very far back. . . [and] the posterior end [is] not vertical but undercut. " (Herrington, 1962: 47)

Measurements (in mm) :

Spec. No.	L	H	H/L	W	W/L
Monument Channel, 20 mi W of Attawapiskat, Ont. (*P. ventricosum* (*s. str.*)).					
1	1·9	1·6	0·84	1·8	0·95
5	1·8	1·7	0·95	1·6	0·89
9	1·7	1·6	0·94	1·5	0·88
13	1·6	1·5	0·94	1·5	0·94
Reindeer Lake, Brochet, Man. (*P. ventricosum* (*s. str.*)).					
1	2·2	1·8	0·82	1·9	0·86
3	2·1	2·0	0·95	1·9	0·90
5	1·9	1·6	0·84	1·5	0·79
7	1·5	1·5	1·0	1·4	0·93
Lake at Bernard Harbour, N.W.T. (*P. ventricosum* form *rotundatum*).					
1	3·3	3·0	0·91	2·5	0·76
2	3·2	2·7	0·84	2·4	0·75
3	3·1	2·5	0·81	2·2	0·71
4	2·7	2·4	0·89	1·9	0·70

Records:

Over 100 lots are available so for some provinces only marginal records are listed. See Map 37.

Quebec. *P. ventricosum* form *rotundatum*: Small pond near Clearwater River, 3/4 mi E of Richmond Gulf. Lac Gabrielle, 10 mi SW of Chibougamau (both this survey).

P. ventricosum (*s. str.*): Lac Aigneau (57°10′N, 70°35′W) (1955, D. R. Oliver!).

Ontario. *P. ventricosum* form *rotundatum*: Small creek 18 mi W of Cochrane. Winisk River, 15 mi S of Winisk (both this survey). *P. ventricosum* (*s. str.*): Klotz Lake, 30 mi E of Longlac. Stout Lake, at outlet (52°08′N, 94°44′W). Pond near Winisk River, 10 mi S of Winisk (all this survey).

Manitoba. *P. ventricosum* form *rotundatum*: Falcon Lake (49°41′N, 95°15′W). Red Sucker Lake, east end (54°10′N, 93°57′W). Brochet Lake (58°35′N, 101°35′W) (all this survey). *P. ventricosum* (*s. str.*): Lake Manitoba, near narrows (1964, M. Ouellet!). Goose Creek, 7 mi S of Churchill. Reindeer Lake, Brochet (both this survey).

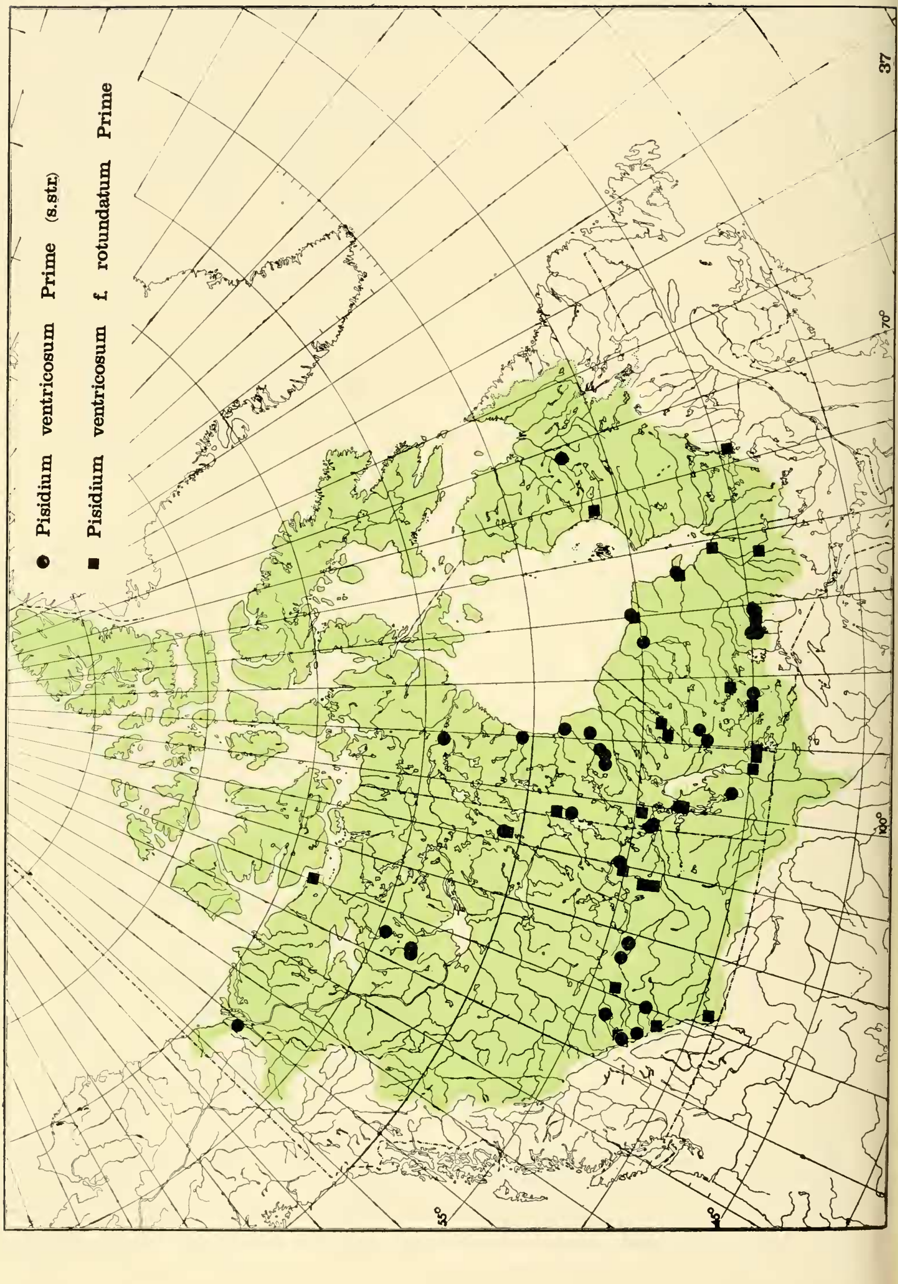
Saskatchewan. *P. ventricosum* form *rotundatum*: Halkett Lake, 20 mi S of Waskesiu Lake. Stream 4 mi N of La Ronge (both this survey). *P. ventricosum* (*s. str.*): Lac la Ronge (1948, 1954, Univ. Sask.!).

Alberta. *P. ventricosum* form *rotundatum*: 43 mi N of Twin Butte (1963, Joyce Cook!). Mildred Lake, Jasper National Park (1954, Can. Wildlife Serv.!). Tawatinaw River, 1 mi N of Rochester (this survey).

P. ventricosum (*s. str.*): Hector Lake, 10 mi NNW of Lake Louise. Whitney Lake, SW edge, 6 mi SE of Lindbergh (both this survey).

Northwest Territories. *P. ventricosum* form *rotundatum*: Wholdaia Lake (60°45′N, 104°30′W) (1959, Fish. Res. Bd.!). Lake at Bernard Harbour (1915, 1916, Can. Arctic Exped.!).

P. ventricosum (*s. str.*): Hyde Lake (66°45′N, 95°22′W) (1959, Fish. Res. Bd.!). Mackenzie River, Aklavik (1957, Fish. Res. Bd.!).


● Pisidium ventricosum Prime (s.str.)
■ Pisidium ventricosum f. rotundatum Prime
37
70°
100°
55°
45°

Distribution: In North America *Pisidium ventricosum* (*s. str.*) and *P. ventricosum* form *rotundatum* have approximately the same geographical range, i.e., Newfoundland, New Brunswick (*ventricosum*), and southern Quebec (*rotundatum*) north and northwest to Ungava and the western Arctic Coast of Canada, west to Alberta, across the northern states from Maine to Washington, and south in the mountains to Utah, Colorado, and Mexico.

Biology and Ecology: The 26 lots of *Pisidium ventricosum* (*s. str.*) collected during this survey are from 12 large lakes, 5 small lakes, 2 permanent ponds, and 7 rivers and streams from over 100 feet to less than 10 feet wide. The 18 lots of *P. ventricosum* form *rotundatum* are from 8 large lakes, 2 small lakes, 3 permanent ponds, and 5 rivers and streams from over 100 feet to about 15 feet wide. Vegetation was present at all localities but of variable abundance. Bottom sediments also varied but were principally of mud. Current in rivers and streams varied from rapid to imperceptible.

There was no discernable difference between the ecology of *Pisidium ventricosum* (*s. str.*) and form *rotundatum* in the Canadian Interior Basin.

Herrington (1962: 47) writes: " The form *rotundatum* is found in sheltered spots in lakes, creeks, and rivers but is most commonly found in ponds and lagoons; it usually takes shelter among dead leaves of trees. The form *ventricosum* is found principally in lakes and large rivers. "

Nothing is known regarding the anatomy or reproduction of this species. For details of the anatomy and reproduction of *Pisidium obtusale* Pfeiffer, a European species which appears to be closely related to *P. ventricosum*, see Odhner (1929: 89).

Remarks: Both *Pisidium ventricosum* (*s. str.*) and its *rotundatum* morph were considered " forms " of *P. obtusale* Pfeiffer by Herrington (1962: 47). In 1965 (p 44) Herrington accepted the view of European workers that *P. obtusale* was distinct, however.

Pisidium (*Cyclocalyx*) *walkeri* Sterki
Plate 19, Fig. 5; Map 38.

P[*isidium*] *walkeri* Sterki, 1895. *Nautilus*, *9*(7): 75. Type locality: " Kent County, Michigan."
Pis[*idium*] *walkeri* var. *mainense* Sterki, 1898. *Nautilus*, *12*(7): 79. Type locality: " different waters near Caribou, Aroostook Co., Maine."

Diagnosis: Shell up to about ¼ inch long, subovate (acentric, anterior produced), inflated, thin-walled, dull to slightly glossy, umbones moderately large and posterio-dorsal, and hinge narrow. Some specimens are like *Pisidium casertanum* but in that species the hinge is parallel with the dorsal margin.

Description: " Shell of medium size, long, moderate diameter, thin walls; beaks far back, rather prominent, narrow; striae medium to somewhat heavy, uniformly spaced; periostracum dull to slightly silky; dorsal margin tilted back, short, openly curved, joining anterior end with small angle and posterior end with greater angle; anterior end a long, slightly curved slope, joining ventral margin quite low with rounded angle; ventral margin very long and not much curved, joining posterior end without angle; posterior end vertical; hinge rather short, light, far back, tilted (not parallel with ventral [sic! dorsal] margin); laterals rather long; cusps moderately sharp; cusps of A1 central or on distal side of centre; of P1 distal, of A2 proximal or on proximal side of centre, of P2 central; cardinals subcentral; C2 short, much curved (sometimes an inverted D); C4 much lighter, short, curved, directed toward interior of shell; C3 parallel with hinge-plate

PLATE 19. *Pisidium* (III)

FIG. 1. *Pisidium subtruncatum*, Lac la Ronge, Saskatchewan (NMC 19008, 3·0 mm), ... p 194.

FIG. 2. *Pisidium variabile*, Manitoba (NMC 1953, 3·5 mm), ... p 197.

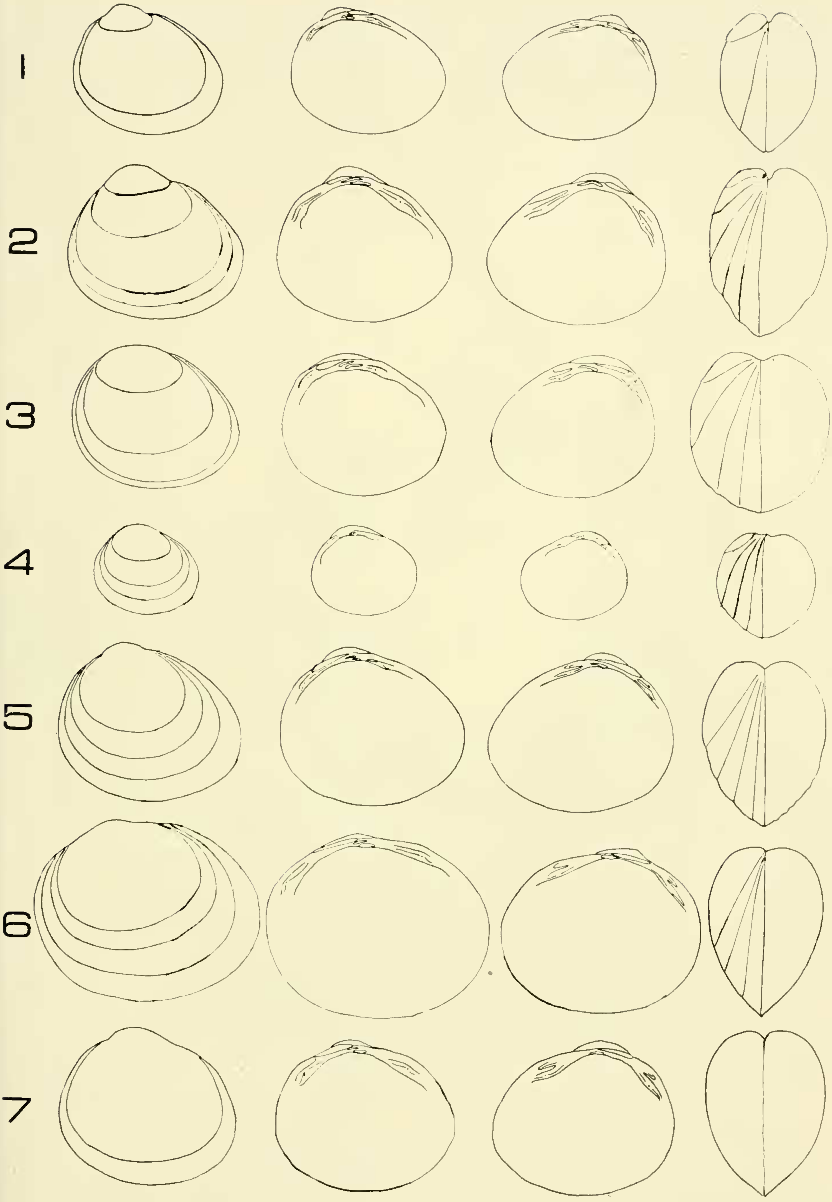
FIG. 3. *Pisidium ventricosum* (*s. str.*), Klotz Lake, near Longlac, Ontario (NMC 19134, 1·5 mm), ... p 200.

FIG. 4. *Pisidium ventricosum* (*rotundatum* morph). small stream near La Ronge, Saskatchewan (NMC 18612, 2·1 mm), ... p 200.

FIG. 5. *Pisidium walkeri*, Lac La Motte, near Vald' Or, Quebec (NMC 15610, 3·7 mm), ... p 203.

FIG. 6. *Pisidium conventus*, Aberdeen Lake, Northwest Territories, (NMC 15532, 2·3 mm), ... p 209.

FIG. 7. *Pisidium punctatum*, Millhaven Creek, near Odessa, Ontario (NMC 15249, 1·9 mm), ... p 212.


1
2
3
4
5
6
7

varying in degree of curvature, its posterior end enlarged.

The form *mainense* is smaller with finer striae, the anterior slope a little more rounded and, usually, beginning a little nearer the beaks. The shell is relatively shorter and, therefore, appears to be higher in outline. The cardinals of the left valve are more nearly parallel (as in *Pisidium subtruncatum*) and C2 is longer than the usual *P. walkeri s.s.*" (Herrington, 1962: 51).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Black River, Matheson, Ont.					
1	3·4	2·8	0·82	2·3	0·68
5	3·3	2·9	0·88	2·1	0·64
9	3·0	2·7	0·90	1·9	0·63
13	2·7	2·3	0·85	1·6	0·59
Lac la Ronge, Sask.					
1	3·5	2·8	0·80	2·1	0·60
5	3·3	2·9	0·88	1·8	0·55
9	3·0	2·6	0·87	1·8	0·60
13	2·8	2·3	0·82	1·5	0·54
Baker Lake, N.W.T.					
1	2·6	2·2	0·85	1·6	0·62
3	2·5	2·1	0·84	1·5	0·60
5	2·4	2·0	0·83	1·4	0·58
7	2·3	2·0	0·87	1·3	0·56

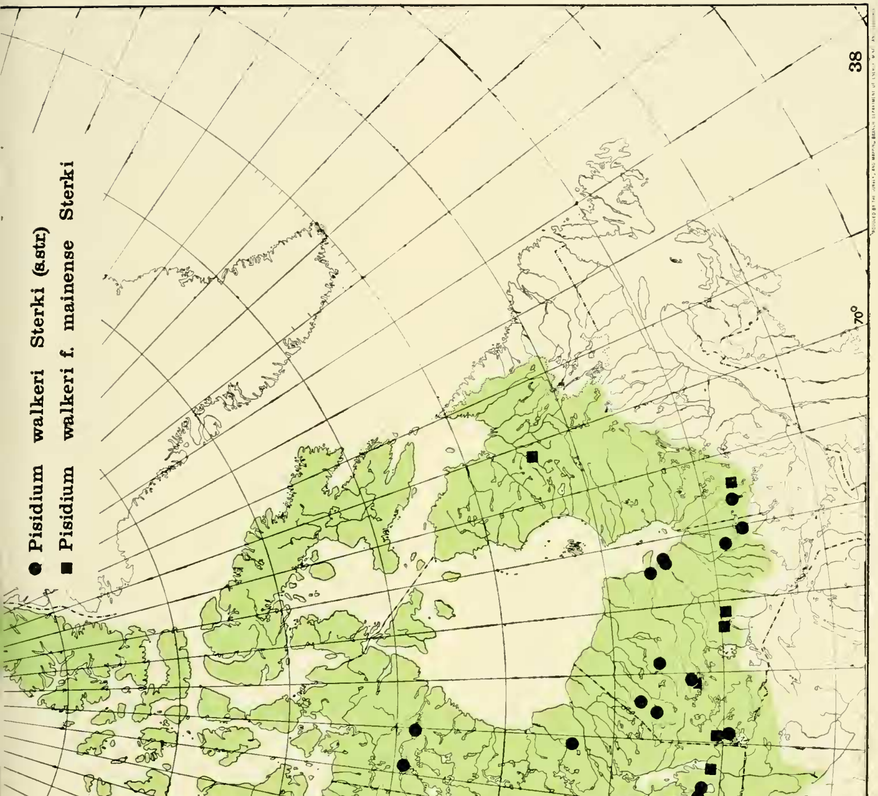
Records:

Quebec. *P. walkeri* (*s. str.*): Lac La Motte, 25 mi NW of Val d'Or (this survey). *P. walkeri* form *mainense*: Lac Aigneau (57°10′N, 70°35′W) (1955, D. R. Oliver!). Lac Pascalis outlet, 13 mi S of Senneterre (this survey).

Ontario. *P. walkeri* (*s. str.*): Black River, Matheson. Abitibi River, 17 mi N of Cochrane. Klotz Lake, 30 mi E of Longlac. Chadwick Lake outlet, 16 mi E of Kenora. Small stream 4 mi W of Pickle Crow. Albany River, 7 mi W and 9 mi W of Fort Albany (2 localities). Attawapiskat River, 6 mi W of Attawapiskat (all this survey). Sachigo Lake (53°49′N. 92°08′W) (1964, Ont. Dept. Lands and Forests!), *P. walkeri* form *mainense*: Kenogamisis Lake, 7 mi SE of Geraldton. Vermilion Lake, Vermilion Bay (both this survey).

Manitoba. *P. walkeri* (*s. str.*): Ebb and Flow Lake, 7 mi NNW of Kinosota (this survey). Lake Manitoba, east side, 1 mi N of Narrows and 15 mi W of Benhorn (2 localities) (both 1964, M. Ouellet!). Cormorant Lake (54°14′N, 100°49′W) (1906, W. McInnes!). Simonhouse Lake (54°33′N; 101°10′W). Recluse Lake (56°55′N, 95°45′W) (both this survey). *P. walkeri* form *mainense*: River at Hwy. 9 just south of Petersfield (this survey).

Saskatchewan. *P. walkeri* (*s. str.*): Montreal Lake (1955, D. S. Rawson!). Lac la Ronge (9 lots from whitefish stomachs) (1952–54,


● Pisidium walkeri Sterki (s.str.)
■ Pisidium walkeri f. mainense Sterki
38
70°
100°
65°
45°

Univ. Sask.!). Hunter Bay, Lac la Ronge (1949, Univ. Sask.!). Waden Bay, Lac la Ronge (25-foot depth) (this survey). Wollaston Lake (1956, Univ. Sask.!).

Alberta. *P. walkeri* (*s. str.*): " The Willows ", Lake Athabasca (whitefish stomachs) (1945, D. S. Rawson!).

Northwest Territories. *P. walkeri* (*s. str.*): Aberdeen Lake, northwest side (64°45′N, 100°00′W) (1961, Elizabeth Macpherson!). Baker Lake, 12 mi S of Baker Lake Settlement (whitefish stomachs) (1962, E. W. Smith, and W. L. Donahue!). Big Buffalo River at Great Slave Lake (Herrington, 1962: 51).

Distribution: *Pisidium walkeri* (*s. str.*) occurs from New Brunswick northwest to James Bay, Aberdeen Lake, N.W.T. and Great Slave Lake, N.W.T. and from Maine south to Virginia, west to Montana, and also in Arizona. In Saskatchewan and Alberta it is known only from the boreal forest region. *P. walkeri* form *mainense* has an overlapping but more easterly range. It extends into northern Quebec and Labrador (Astray Lake) and is not yet recorded from Alberta, Saskatchewan, northern Manitoba, the Northwest Territories or in the United States west of Michigan (Herrington, 1962: 51 and this survey).

Biology and Ecology: The 12 lots of *Pisidium walkeri* (*s. str.*) collected during this survey came from 5 large lakes, 5 rivers over 100 feet wide, 1 river about 50 feet wide and 1 stream approximately 20 feet wide. Vegetation was present at all but 2 localities and of medium density at most. Substrates were various with mud occurring alone or in part at 8 stations. Current in 6 of the rivers and streams was slow, in the other it was moderate.

The 5 lots of *Pisidium walkeri* form *mainense* from this survey were derived from 3 large lakes and 2 slow-flowing rivers, with widths of 75 and 30 feet. Vegetation was moderate to thick at all localities and substrates were of gravel and sand at 1 locality, sand at 1, sand and mud at 1, and mud at 2.

According to Herrington (1962: 51) the habitat of this species is as follows: " Creeks, rivers, and small lakes. Scarce and usually not abundant in any 1 place. *Pisidium walkeri* form *mainense* is found in bodies of water having a soft bottom. From the 19 stations that had yielded the specimens of the form *mainense* in my collection, 17 were small lakes or ponds; there was 1 creek and 1 small river. It is found in relatively few places, but is abundant in some small lakes that are filling up with shells and marl. "

The present data do not indicate the existence of any ecological differences between *Pisdium walkeri* (*s. str.*) and its form *mainense*; they also extend the habitat range of both to include large lakes and large rivers.

Heard (1965: 395) found that *Pisidium walkeri* from Ore Creek, Livingston County, Michigan reproduce like other species of *Cyclocalyx*. Gametogenesis was most active in late summer and early fall and mature gametes occurred most abundantly in winter and early spring. The normal individual life span was about 1 year with a single brood born each spring. Nothing has been published on the anatomy of this species.

Subgenus *Neopisidium* Odhner

Neopisidium Odhner, 1921: *J. Conchol.*, *16*(7): 222. Type species: *Pisidium conventus* Clessin, by subsequent designation (Odhner, 1938: 233, 237).

Shell relatively very small (up to 3 mm) and retaining juvenile characters in the adult. " Complete absence of branchial siphon; posterior gills entirely lacking; [and] dorsal loop or lobe of the nephridia united..." (Heard, 1965: 383). Extent of life span in North America unknown. Two small litters are produced each year (Heard, 1966: 87).

Five North American species have been included in this group: *Pisidium conventus* Clessin, *P. cruciatum* Sterki, *P. insigne* Gabb. *P. punctatum* Sterki and *P. punctiferum* Guppy, but only *P. conventus* and *P. punctatum* occur in the research area.

Pisidium (*Neopisidium*) *conventus* Clessin
Plate 19, Fig. 6; Map 39.

Pisidium conventus Clessin, 1877: *Malak. Blätt.*, *24*: 181, pl. 3: 7 (not seen). Type locality: Lake of Starnberg, Bavaria.

Diagnosis: Shell up to about $\frac{1}{8}$ inch long, thin, fragile, subovate, not inflated, with dull gloss, umbones low and nearly central, shell porous " but the canaliculi run parallel with the shell surface and often branch, a character peculiar to *P. conventus* " (Ellis, 1940: 58). Cardinal teeth overhang hinge plate, lateral teeth lamellar and with distal cusps, distance between lateral and cardinal teeth relatively great, and hinge plate relatively longer than in any other *Pisidium*.

Description: " Shell small, thin; specimens vary greatly in outline when occurring in deep water of small lakes, or in large lakes; shells from small lakes of high altitude tend to be larger and less angular; beaks subcentral to somewhat posterior, broad and not prominent; in some specimens there is a flattening, the beginning of a wrinkle or ridge; striae fine, but usually even and distinct; periostracum dull to a dull gloss; the so-called " rest periods " are distinct, evenly spaced and like those in some small-creek specimens of *P. casertanum*; dorsal margin rather long, openly curved, with something of a bend at the beaks; anterior end a long slope, sometimes rounded; posterior end frequently sloped at same angle as anterior end, but sometimes more rounded, and even vertical; ventral margin gently curved; hinge usually slightly bent at beaks, long, and the plate narrow; laterals long and slender; cusps of A1, P1, and A2 distal or on distal side of centre, of P2 distal; cardinals central or subcentral; C2 at or on proximal end of A2, short, close to inner edge of hinge-plate or overhanging and either about parallel with hinge-plate or with posterior end slightly more interior; C4 slightly longer than C2, slimmer, straight or slightly curved, beginning above centre of C2 and parallel with it, or its posterior end directed a little more toward the interior; C3 moderately long, slightly curved, almost parallel with hinge-plate, posterior end enlarged somewhat, therefore, nearer inner edge of hinge-plate. " (Herrington, 1962: 36).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Hunter Bay, Lac la Ronge, Sask.					
1	1·9	1·3	0·68	1·0	0·52
5	1·8	1·4	0·78	0·8	0·44
9	1·7	1·4	0·82	0·8	0·47
13	1·5	1·3	0·87	0·9	0·60

Spec. No.	L	H	H/L	W	WL
Aberdeen Lake, northwest side, N.W.T. (64°45′N, 100°00′W).					
1	2·6	2·0	0·77	1·5	0·58
5	2·4	2·0	0·83	1·5	0·63
9	2·2	1·5	0·68	1·4	0·64
13	2·0	1·7	0·85	1·2	0·60
Lake at Bernard Harbour, N.W.T.					
1	2·7	2·3	0·85	1·7	0·63
5	2·6	2·2	0·85	1·7	0·65
9	2·5	2·2	0·88	1·5	0·60
13	2·2	1·5	0·68	1·3	0·59

Records:

Quebec. Lake Aigneau (57°10′N, 70°35′W) (1955, D. R. Oliver!). Lake Abitibi, Baie la Sarre, 3 mi WNW of Palmarolle (this survey).

Ontario. Lake St. Joseph (51°05′N, 90°35′W) Sutton Lake (54°15′N, 88°44′W) (1963 and 1961, both Ont. Dept. Lands and Forests!). Lake Nipigon (Herrington, 1961: 9).

Saskatchewan. Hunter Bay, Lac la Ronge (1948–49, Univ. Sask.!). Reindeer Lake, Wollaston Lake, and Cree Lake (Heard, 1963a: fig. 1). Camsell Portage, Lake Athabasca (1945, Fish. Res. Bd.!).

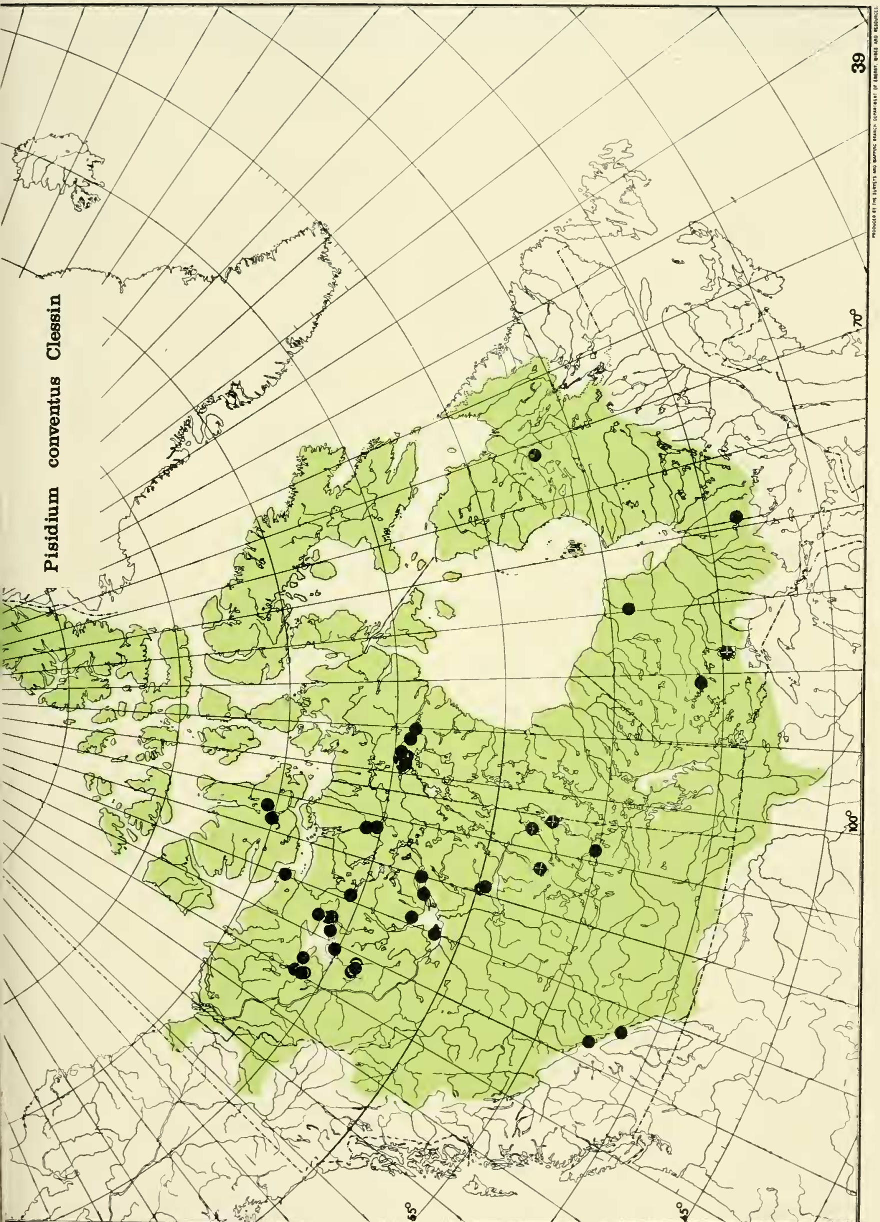
Alberta. Edith Lake, Jasper National Park (1954, Can. Wildlife Serv.!).

Northwest Territories. Baker Lake, 12 mi S of Baker Lake settlement (1962, E. W. Smith & W. L. Donahue!). Aberdeen Lake, northwest corner (64°45′N, 100°00′W) (several lots) (1961, Elizabeth Macpherson!). Beechey Lake (65°25′N, 106°50′W) (1959, Fish. Res. Bd.!). "Namaycush Lake" (70°46′N, 108°34′W) and "Zeta Lake" (71°00′N, 106°38′W). Victoria Island (both 1962, Fish. Res. Bd.!). Lake at Bernard Harbour (1915, 1916, Can. Arctic Exped.!). Redrock Lake (65°28′N, 114°10′W) (1959, W. B. Scott!). Great Slave Lake at Yellowknife Bay, Tochatini Bay, and Ykama Bay (1944, 1946, D. S. Rawson!). Keller Lake (63°55′N, 121°35′W) (1962, L. Johnson!). Great Bear Lake at 11 localities (1963–1965, Fish. Res. Bd.!).

Distribution: Great Lakes—St. Lawrence River drainage area northward throughout subarctic and arctic mainland Canada and on Victoria Island (see "Records"); west to Unimak Island, Aleutian Islands; and south in mountain lakes in Montana and Washington. The species also occurs in lakes in northern Eurasia, i.e., Scotland and the Scandinavian countries to Siberia, including Novaya Zemlya; also in alpine lakes in Germany, Austria, and Switzerland (Odhner, 1923: 3; Heard, 1963a: 79).

Biology and Ecology: All subarctic and arctic collections here reported, which have data on method of capture, are from the stomachs of whitefish or lake trout. Heard (1963a) has published a detailed account of the biology and ecology of this species; the following comments are based on that report.

The species is most frequently met in cold subarctic, arctic, or alpine lakes, but it has also been found in swamps near Grange-in-Barrowdale, Cumberland, England and near Ward, Montana. In lakes it is ordinarily absent from shallow depths and has been found as deep as 219 m in Great Slave Lake and 230 m in Loch Ness, Scotland. Suitable substrates are various and include mud, sand, and (occasionally) stones.


Pisidium conventus Clessin
39
70°
100°
65°
45°

Specimens from Lake Superior were found to feed on several species of diatoms. The size of embryos contained indicated that 2 broods are produced, 1 in summer and 1 in winter. Up to 10 embryos were found in a single adult, the average number being about 6. For further details see Odhner (1923) and Heard (1963a).

Pisidium (*Neopisidium*) *punctatum* Sterki
Plate 19, Fig. 7; Map 40.

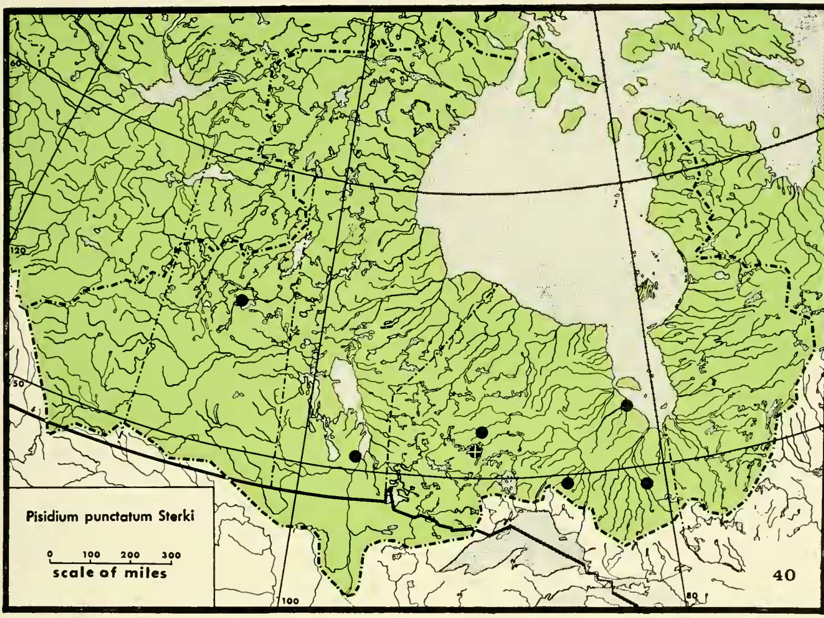
Pisidium punctatum Sterki, 1895: *Nautilus*, *8*(9): 99. Type locality: " Ohio; Tuscarawas River, Bear Run, tributary to the Mahoning River, Portage Co., [and] a spring brook at Rootstown Station, Portage Co., emptying into the Cuyahoga River (Lake Erie and St. Lawrence drainage)."

Diagnosis: Shell up to about 1/10 inch long, subovate, inflated, walls of moderate thickness, and (in some specimens) with a horizontal ridge on the umbones. The shell is full of tiny holes or punctae, visible on both the inside and outside (at 25x or 50x) but especially on the inside.

Description: " Shell minute, inequipartite, high, oblique, strongly ventricose, almost globular, regularly and sharply striated, microscopically rugulose, whitish; anterior part moderately long, the edge above oblique, almost straight, end slightly angled, rather inferior; anterior part short, truncate, slightly angular above, rounded below; superior and inferior margins moderately curved, the former rather short, the latter long; scutum little, scutellum moderately marked, both forming slight angles; vertical section heart-shaped, horizontal, short, lanceolate-rhombic; margins very slightly acute; beaks moderately full and prominent, with a longitudinal, slightly, oblique ridge (sometimes obsolete) below the culmination; nave [nacre] moderately thick, whitish, with crowded, small pits, from which it appears as if dotted; hinge moderately strong; cardinal teeth fine, in the left valve two, lamellar, longitudinal, about equally long, a little curved, almost parallel, the upper little anterior; in the right valve one longitudinal, little curved, lamellar, the posterior end slightly thickened; lateral teeth rather small and thin, in the left valve one, pointed, in the right valve two, the outer quite small; hinge-line fine, rather regularly formed; ligament rather long and fine." (Sterki, 1895: 99).

Measurements (in mm):

Spec. No.	L	H	H/L	W	W/L
Small stream 4 mi W of Pickle Crow, Ont.					
1	1·7	1·6	0·94	1·2	0·71
2	1·6	1·5	0·94	1·1	0·69
3	1·5	1·3	0·87	1·0	0·67
4	1·5	1·4	0·93	1·0	0·67
Lac la Ronge, Sask (from whitefish).					
1	1·7	1·4	0·82	1·0	0·59
3	1·6	1·4	0·88	0·9	0·56
5	1·5	1·4	0·93	1·0	0·67
9	1·4	1·3	0·93	0·8	0·57



Records:

Ontario. Klotz Lake, 30 mi E of Longlac. Small stream 4 mi W of Pickle Crow. Inlet of Albany River, 7 mi W of Fort Albany (all this survey). Hamilton Lake (51°51′N, 90°28′W) (Baker & Cahn, 1931: 47).

Manitoba. River south of Petersfield at Hwy. 9 (this survey).

Saskatchewan. Lac la Ronge, from whitefish (1954, Univ. Sask.!).

Distribution: Northern United States and southern Canada from Ontario to Saskatchewan (see above). The southern limit of its range is not known although in the southern United States *Pisidium punctatum* is absent. A similar but distinct species occurs there, viz., *P. punctiferum* Guppy (Herrington, 1965: 44; Heard, 1966: 87).

Biology and Ecology: This rare species was collected on only 5 occasions during this survey. Two collections were made on different dates from 1 large lake (Klotz Lake, Ont.), 1 was from a backwater of a large river (Albany River), and 2 were from slow-flowing streams, each about 25 feet wide. Vegetation was thick and the substrate was mud at 4 localities. The 5th locality (Albany River) had sparse vegetation on July 10, 1965 and the substrate was gravel and clay. Vegetation was not yet fully grown at that subarctic locality on that date, however.

According to the scattered literature (see La Rocque 1967: 328; northern records only) *Pisidium punctatum* occurs in rivers and lakes. No detailed ecological data are available.

Specimens from a tributary of White Oak Creek, Tennessee were studied by Heard (1965: 99) and were found to bear 2 litters per year. Litter size varied from 4 to 18 in May and 2 to 12 in November. All embryos in the

same adult were of about the same size but between litters they varied from about 0·1 to 0·8 mm in length at the time of examination.

Class Gastropoda

This is the most diverse class of Mollusca. It contains about 300 living families and nearly 100 extinct families (Taylor & Sohl, 1962). Most species possess spiral shells but some have limpet- or saucer-shaped shells and others (slugs and nudibranchs) are without shells. The mouth in most groups is fitted with a chitinous plate or plates (the jaw) and with a radula. The radula is a strap-like structure bearing numerous transverse rows of chitinous teeth used principally for rasping food into small particles during feeding. The arrangement and number of radula teeth in each transverse row, the configuration of individual teeth, and the number and shape of cusps provide reliable taxonomic characters at the ordinal, familial, and generic level and in some instances at the specific level.

Torsion is the fundamental evolutionary event which, in the early Palaeozoic, gave rise to Gastropoda from bilaterally symmetrical ancestors. It involves displacement of the viscera, mantle, and shell in a 180° counter-clockwise twist with respect to the head and foot. This places the mantle cavity in front and in a more functional position behind the head and results in twisting the visceral loop into a figure 8 (see Yonge, 1960: 12). The process of torsion can still be observed during the larval development of some relatively primitive marine gastropods, e.g., in *Haliotis*, *Acmaea*, *Patella* and *Trochus*.

Recent authors subdivide Gastropoda principally by 2 systems, 1 (e.g., see Hyman, 1967) based initially on the presence or absence of either ctenidia or a pulmonary sac and the other (e.g., see Taylor & Sohl, 1962) either on the persistence of evidence for torsion or of secondarily evolved detorsion. In the older and more familiar system the subclasses Prosobranchia, Opisthobranchia, and Pulmonata are recognized while in the other the subclasses Streptoneura (=Prosobranchia) and Euthyneura (=Opisthobranchia+Pulmonata) are used. In the present work the names Prosobranchia and Pulmonata are give preference but both systems are recognized.

Subclass Prosobranchia (Streptoneura)

Most prosobranchs possess an operculum, breathe by means of gills or ctenidia, have separate sexes, and have only 1 pair of tentacles. See the superb monograph by Fretter & Graham (1962) for details of the functional morphology of prosobranchs. The subclass is divided by many authors into 3 orders, viz., Archaeogastropoda, Mesogastropoda, and Neogastropoda. That system is followed here.

The Archaeogastropoda are principally marine but have a few terrestrial and freshwater representatives. They are an ancient and primitive order with diffuse nervous systems, mainly nacreous shells, and opercula which may be calcareous or chitinous. Radulae of Acmaeidae and Patellidae are docoglossate, i.e., with paired teeth, the "formula" for each transverse row being approximately 2-2-2-2. In the other families the radulae are rhipidoglossate i.e., with the formula 'many'-6-1-6-'many'.

The Mesogastropoda live in marine, terrestrial, and freshwater environments. Their nervous systems are also diffuse but almost all possess non-nacreous shells and non-calcareous opercula. The radulae are taenioglossate and have the general formula 2-1-1-1-2.

The Neogastropoda are all marine. They have concentrated nervous systems,

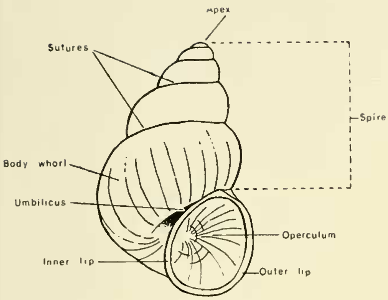


FIG. 7. Exterior morphology of a prosobranch gastropod shell.

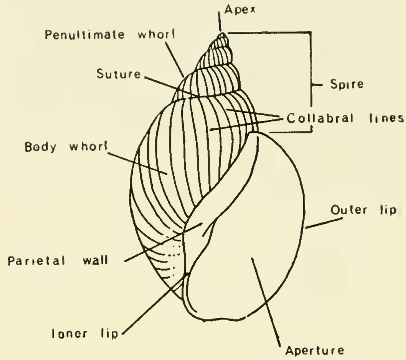


FIG. 8. Exterior morphology of a pulmonate gastropod shell.

a proboscis which contains the radula, a distinct siphonal canal at the base of the aperture, and are operculate or non-operculate. The radulae are rachiglossate (formula 1-1-1) or toxoglossate (formula 1-0-0-0-1 or 1-1-1-1-1).

Order Mesogastropoda

The 3 superfamilies of operculate freshwater gastropods living in the Canadian Interior Basin, i.e., the Viviparacea, Valvatacea, and Rissoacea, are all members of this Order. Sexes are separate in most mesogastropods. In Valvatacea the sexes are united, however, and in Viviparacea (genus *Campeloma*) reproduction in northern species is parthenogenetic and males are absent. Viviparacea do not deposit external egg masses but retain the eggs and young in the brood pouch until the juveniles are partly grown. Valvatacea and Rissoacea deposit individual encapsulated eggs.

Superfamily Viviparacea

Following Taylor & Sohl (1962), this superfamily is considered to include 2 families, viz., Viviparidae and Ampullariidae. The shells of both are similar, i.e., medium-sized to large, conispiral or (in some Ampullariidae) planispiral, and both have corneous, paucispiral opercula. The families differ in anatomy, behaviour, and reproductive characters, however, Viviparidae being ovoviviparous and Ampullariidae being oviparous. Only Viviparidae occur in the Canadian Interior Basin.

Family VIVIPARIDAE Gray

Viviparidae J. E. Gray, 1847: *Proc. zool. Soc. London, 15*: 155. Type genus: *Viviparus* Montfort, 1910. Information supplied by W. J. Clench (pers. comm., Dec., 1968). Paludinidae Gray (*in* Turton), 1840 (p 89) is a *nomen oblitum*.

Shells moderately large to large, orthostrophic, conispiral, holostomatous, non-umbilicate or with a small umbilicus, thin to thickened, subinflated to inflated and smooth or highly sculptured (*Tulotoma*). Operculum large, corneous, and paucispiral. Some species are monoecious, others are dioecious, and all are ovoviviparous. Some species are also known to be omnivorous and to feed on

dead animal and plant material but the feeding habits of others are unknown.

" Animal with a long snout, not divided into tentacular lobes; tentacles long and slender, in the male the right one is shorter, truncated and forms a sheath for the verge; eyes on peduncles on the exterior base of the tentacles; mantle with two cervical lobes, of which the right is the larger, forming with the mantle distinct tubular conduits for the ingress and egress of water [and air when at the surface] for respiration; jaws two; radula with [usually seven] teeth simple or denticulate, central tooth large, broad, without basal denticles, laterals large, subtrigonal, marginals narrow, elongated..." (Walker, 1918: 24).

Although the Viviparidae are worldwide in distribution they are most numerous in tropical and warm-temperate regions. Geologic age: Carboniferous (possibly) or Jurassic to Recent (Wenz, 1939: 489).

Genus *Campeloma* Rafinesque

? *Ambloxis* Rafinesque, 1818: *Amer. Monthly Mag.*, *3*: 355 (Binney & Tryon reprint, 1864: 23). Two species included: *A. eburnea* and *A. ventricosa*, both *nomena nuda*.

Campeloma Rafinesque, 1819: *J. Phys. Chim. Hist. natr.*, *88*: 423 (Binney & Tryon reprint, 1864: 26). Type species: *C. crassula* Raf., by monotypy.

Melantho Bowditch, 1822: *Elements of Conchol.*, Paris, p 27, pl. 6, fig. 15. No species or locality cited.

Shells medium to large, of moderate to pronounced thickness, dextral (rarely sinistral), orthostrophic, conispiral, non-umbilicate, almost smooth except for lines of growth, and with impressed sutures and rather rounded whorls. Aperture ovate, inner lip more or less sinuous, outer lip simple. Operculum horny, concentric, with nucleus on the left of centre, and when withdrawn filling the aperture entirely. Foot large, truncate anteriorly and rounded posteriorly; eyes on peduncles at outer base of tentacles; 2 horny jaws present, 1 on either side of the mouth; radula taenioglossate, formula normally 2-1-1-1-2; omnivorous; and ovoviviparous.

Species in Canada and northern United States lack males and reproduce parthenogenetically, but in at least some more southern species males are present and reproduction is sexual (van der Schalie, 1965). In the southern region males are smaller than females and have their right tentacles enlarged and modified to form a functional penis. For additional details see Baker (1928a: 52, anatomy), Van Cleave & Altringer (1937: 167, reproduction and life history), Clench (1962: 273, taxonomy), and Anderson (1966, reproduction and taxonomy).

Approximately 17 species are currently recognized in the genus *Campeloma*. These are distributed throughout eastern North America from the Gulf of Mexico to the south-central part of the Canadian Interior Basin. Geologic range: Upper Cretaceous to Recent.

Campeloma decisum (Say)
Plate 11, Fig. 1; Plate 21, Figs. 1, 2; Map 41.

Limnaea decisa Say, 1816: *Nicholson's Encyclopedia*. 1st Amer. ed. (no pagination), pl. 2, fig. 6 (Binney reprint 1858: 49, as *Paludina decisa*). Type locality not cited but probably Delaware River.

? *Paludina integra* Say, 1821: *J. Acad. natr. Sci. Philad.*, 2: 174 (Binney reprint, 1858: 69). Type locality: " waters of the Missouri." See synonymy under *Cincinnatia cincinnatiensis* (p 241).

? *Paludina milesii* Lea, 1863: *Proc. Acad. natr. Sci. Philad.*, p 156. Type locality: " Branch Lake, Antrim Co., Michigan."

? *Campeloma leptum* Mattox, 1940: *Nautilus*, 54(1): 12, pl. 1: 1–3. Type locality: " Mill Pond near St. Thomas, Ontario, Canada."

? *Campeloma tannum* Mattox, 1940: Loc. cit., p 15, pl. 1: 4–6. Type locality: " Speed River near Hespler, Ontario."

Diagnosis: Shell up to about $1\frac{1}{3}$ inches long, elongate-ovate, thick, apex decollated by corrosion (in specimens from

soft water), and with brown periostracum and a corneous operculum.

Description: Shell up to about 34 mm long and 22 mm wide, thick, obconic, olive-brown in colour, and with an ovate-auriculate aperture (angled above) which is about half the height of the shell. Whorls about $6\frac{1}{2}$ in uncorroded specimens, convex, narrowly shouldered, and separated by incised sutures. Spire conic, produced at an angle of about 45°-50°, and decollated by corrosion in post-juvenile specimens from soft water; acute and slightly convex in uncorroded specimens. Aperture white to bluish-white within, holostomatous, and mostly basal. Outer lip sharp; inner lip callus reflected and adnate to previous whorl leaving no umbilical opening. Periostracum pale yellowish-brown or olive-brown. Sculpture consisting of numerous fine collabral lines; prominent, irregularly-spaced, dark growth rests; and fine spiral lines. Operculum thin, corneous, auriculate, concave, with nucleus acentric and adaxial, and with numerous concentric lines of growth.

Measurements (in mm):

Spec.	H*	W*	W/H	BH*	W/BH	ApH†	ApW†	ApW/ApH	Whorls
Red River, Abercrombie, N.D.									
1	33·3	19·2	0·577	23·5	0·817	12·7	9·1	0·717	6·3
2	30·0	18·2	0·607	22·0	0·827	12·9	9·2	0·713	6·5
3	25·9+(‡)	16·8	—	19·3	0·870	9·8	7·5	0·765	5·1+(‡)
4	22·7	15·5	0·683	17·2	0·882	9·3	7·0	0·753	5·7
5	22·8	14·0	0·613	16·8	0·833	10·0	6·8	0·680	5·8
6	19·1	12·6	0·660	14·8	0·851	9·0	6·2	0·689	5·5
7	17·6	11·9	0·676	13·7	0·869	8·9	6·8	0·764	5·8
Chukuni River, 3 mi E of Red Lake, Ont. (2 collections).									
1	34·2	22·0	0·641	24·8	0·887	13·9	9·9	0·712	4·8
2	31·7	19·4	0·612	23·6	0·822	13·0	7·8	0·600	4·6
3	30·5	20·1	0·659	22·8	0·881	12·2	8·9	0·729	4·3
4	30·4+	19·8	—	23·5	0·843	13·2	9·6	0·727	4·2+
5	28·7+	18·9	—	21·2	0·891	11·5	7·9	0·686	4·0+
6	27·6	18·8	0·681	20·6	0·912	11·2	6·7	0·598	4·5
7	27·5+	19·5	—	21·7	0·899	11·4	10·5	0·921	4·0+
8	22·4+	15·4	—	16·9	0·911	9·3	6·8	0·731	3·8+
9	21·6	14·9	0·689	17·1	0·871	9·5	6·4	0·673	4·0+
10	21·3+	15·1	—	16·9	0·893	8·0	7·0	0·875	3·7+

* BH is length (or height) of body whorl. All Measurements are in mm.

† Aperture dimensions are measured inside the aperture. The ApW, for example, is the distance between lines parallel to the axis of the shell, one passing through the abaxial extremity of the aperture and the other passing through the adaxial extremity.

‡ A plus sign indicates that early whorls have been eroded. The measurements and whorl counts apply to the remaining portion.

Feature	N	Range	Mean	S.E.$_M$	S.D.
H	30	18·9 —26·6+	23·40	—	—
W	30	13·0 —17·3	15·25	—	—
W/H	30	0·616— 0·705	0·654	·004	·021
BH	30	15·8 —20·2	17·63	—	—
W/BH	30	0·820— 0·923	0·865	·004	·024
ApH	30	8·3 —11·9	10·33	—	—
ApW	30	5·4 — 7·6	6·72	—	—
ApW/ApH	30	0·559— 0·722	0·651	·007	·038
Whorls	30	4·0 — 5·0	4·48	—	—

Records:

Specimens examined are noted as "*decisum* morph" (=apex corroded) or "*integrum* morph." (=apex complete).

Winnipeg River system. Northern Light Lake, Ont. (48°16′N, 90°39′W) (*decisum* morph) (1931, A. R. Cahn!). Basswood River, Ont. (Baker, 1939b: 91). Fort Francis, Ont. Rainy River, Ont. (both Mozley, 1938: 115). Lake of the Woods, Man. ("Hanham" Dall, 1905: 125). Lake of the Woods, McPherson Island (Baker, 1939b: 91). Chukuni River at Hwy. 125, 3 mi E of Red Lake, Ont. (aberrant population, see "Remarks"). Chukuni River at Hwy. 105, 23 (road) mi SE of Red Lake (*decisum* morph). Whitemouth River, Whitemouth, Man. (*integrum* morph). (Both this survey). Whitemouth River, 2 mi N of Whitemouth (*integrum* morph) (1951, W. E. Godfrey!). Whiteshell River, below White Lake and below Betula Lake, Man. (both Mozley, 1939: 114). Winnipeg River, 3 mi E of Fort Alexander, Man. (*decisum-intergum* intermediate morph) (this survey).

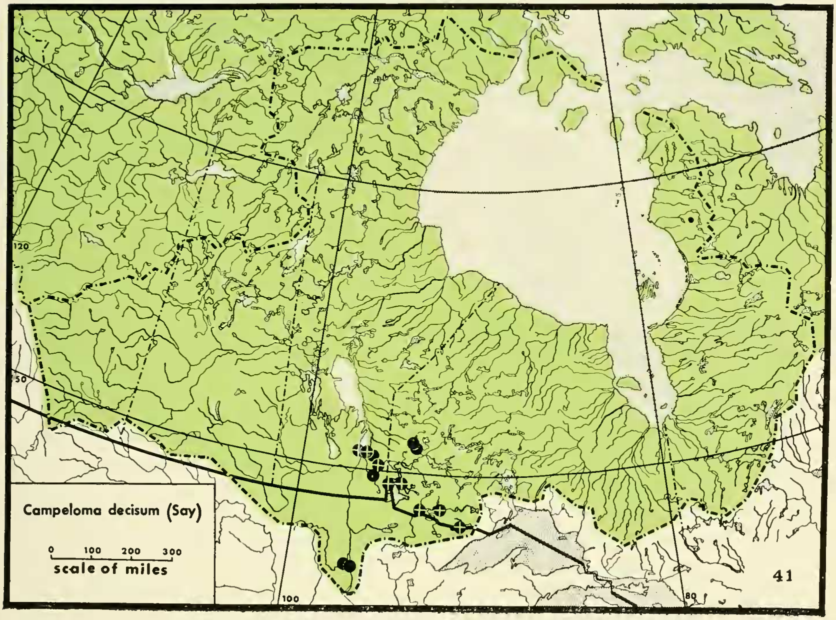
Red River system. Red River, Abercrombie, N.D. (*integrum* morph). Sheyenne River, 1 mi E of Kindred, N.D. (*integrum* morph) (both this survey).

Nelson River system. Lake Winnipeg, Grand Beach, Man. and Grand Marais, Man. Berens River, several miles above junction with Etomami River, Man. (all Mozley, 1939: 114).

Distribution: Eastern North America from Nova Scotia south along the Atlantic Coastal Plain; southern limit unknown. Clench & Turner (1956: 115) consider the populations living from the Suwannee to the Escambia river systems to be *Campeloma geniculum* (Conrad). Westward *C. decisum* extends throughout the Great Lakes- St. Lawrence River system and into adjacent parts of the Canadian Interior Basin at least as far north as Berens River (52°20′N). See "Remarks."

Biology and Ecology: *Campeloma decisum* was found at 6 localities during this survey, as follows: 1 is a large cove marginal to a very wide, slow-flowing river (Winnipeg River) and 5 are moderate to slow-flowing rivers varying from 50 to 200 feet in width. Bottom sediments were mud or clay except at one locality (Chukuni River 3 mi E of Red Lake) where *Campeloma* occurred in silt-filled cracks in large rocks. Aquatic vegetation was moderate or sparse at each locality. South of the Canadian Interior Basin, *C. decisum* is commonly found in lakes or in slow-flowing streams, burrowing just under the surface of a muddy substrate. Dense populations are often found in mud near wharves and promontories used by fishermen. Here the substrate is often enriched by fish entrails and discarded bait.

The soft parts of *Campeloma decisum* have been described by Baker (1928a: 59). *C. decisum* reproduces parthenogenetically and young are held within the uterus after hatching and until the 3 whorl stage of growth is reached. Sinistral specimens are frequently found



in the uterus but these reach adulthood very rarely, i.e., less than one adult in a thousand is sinistral. According to Baker (loc. cit.) the radula, which has the formula 2-1-1-1-2, bears a central tooth which is longer than wide and has tiny cusps near the apices of all teeth.

Remarks on an Anomalous Population: The 2 specimens collected alive on August 24, 1961 from the Chukuni River, 3 mi E of Red Lake, Ontario, have radulae whose formulae are 1-1-1-1-1 instead of the usual 2-1-1-1-2. Their habitat in mud-laden cracks of large rocks is also anomolous. The population is isolated, being the most northerly one known from the Winnipeg River system.

The locality was revisited on July 15, 1969 and a thorough search was made. The snails occurred just off a point of land used by fishermen and were found in the cracks of flat, sloping rocks at depths of 6 to 30 inches. Only 8 specimens could be found (2 were replaced) and all were within a rocky area about 15 feet long and 8 feet wide. The water hardness at this locality measured 30 p.p.m. Radulae were examined from 3 of the 6 specimens retained. Two had formulae of 1-1-1-1-1. One had transverse rows over one half with a 1-1-1-1-1 formula and over the other half with a 2-1-1-1-2 formula.

A very large *Campeloma* population was found downstream in the Chukuni River 23 road miles SE of Red Lake. Water hardness there measured 38 p.p.m. Four specimens were examined for radula characteristics and all had the normal 2-1-1-1-2 arrangement.

It seems probable that the more northerly population has resulted from

a single mutation perpetuated by parthenogenesis and protected from competition by isolation. Although it is certainly anomalous no separate taxonomic status is here proposed.

Remarks on Synonymy: On shell characters it is tempting to follow Tryon (1870: 28) and to synonymize *Campeloma milesii* (Lea), *C. integrum* (Say) and *C. decisum* (Say). Specimens of *Campeloma* from lime-rich water have heavy shells and uncorroded apices while those from lime-poor water have thinner and deeply corroded, decollated shells. Similar responses to hard and soft water are characteristic of unionids, for example, and no one has seriously suggested that such ecophenotypes are separate species. Populations from Canadian Shield localities are of the corroded (i.e., *decisum*) morph while those from lime-rich regions are of the heavy, uncorroded, (i.e., *integrum*) morph. *C. milesii*, supposedly more elongate than *C. decisum* appears to fall well within the normal range of variation for the *integrum* morph.

However, on the other hand, *Campeloma* species, like other large operculate snails, are not easily transported from one drainage system to another except by man. For example *C. decisum* occurs throughout the Ottawa River system even in the northernmost headwaters, the Bousquet River, but not in adjacent, interdigitating parts of the Harricanaw River system. Even within a single large drainage system gene flow between distant populations must be exceedingly slow or, between parthenogenetic populations, non-existent. It therefore seems probable that physiological or other differences have evolved, e.g., between populations from New Jersey and populations from Western Ontario but that such changes are as yet unrecognized. For this reason the identity of *C. integrum* (and of *C. milesii*) with *C. decisum* has been suggested but not asserted.

Campeloma leptum and *C. tannum* differ from *C. decisum* and *C. integrum* by trivial characters only. They are certainly not distinct species but are simply slightly aberrant populations of *C. integrum* (and probably of *C. decisum*).

Viviparidae erroneously recorded from the Canadian Interior Basin

Viviparus intertextus (Say) has been recorded by Clench & Fuller (1965: 397) from Rainy Lake, Minnesota. This record is based on 5 specimens (Pl. 21, Fig. 3) now in the Academy of Natural Sciences (Cat. No. 124, 657) and originally in the collection of Charles M. Wheatley, a well-known 19th century conchologist. The original label reads " near Rainy Lake, Minn. " and " from James ".

It is extremely doubtful that these specimens actually came from Rainy Lake or its drainage area. A.R. Cahn collected extensively in that region and did not find *Viviparus intertextus* (see Baker 1939b: 87). Other competent collectors have also worked in that region and have not found it. *V. intertextus* has been recorded from several localities in the Mississippi River drainage area (Clench & Fuller, loc. cit.) but there are no other records of it from the Canadian Interior Basin and there are none from the St. Lawrence River drainage area, the headwaters of which are close to the Rainy Lake region. In consideration of this and of the fact that the distribution of species of Viviparidae is characteristically restricted by drainage area boundaries, if the original data are at all correct, it is likely that the specimens came from the upper Mississippi River system. Headwaters of that system are in Minnesota about 80 mi south of Rainy Lake.

Superfamily Valvatacea

The superfamily Valvatacea contains only the family Valvatidae, described below.

Family VALVATIDAE Gray

Valvatidae Gray, 1840: (*in*) Turton, *Manual of Land & Freshwater Shells of the British Islands*. 2nd ed., p 79. Type genus: *Valvata* Müller, 1774. Valvatidae has been placed on the Official List of Family-Group Names in Zoology (Name No. 54) by Direction 27 of the International Commission on Zoological Nomenclature, 1955.

Shells small to medium-sized; dextral; orthostrophic and conispiral or planispiral; umbilicate; whorls rounded and either smooth, with collabral sculpture, or carinated; and aperture complete and circular except where modified by carinae. Operculum horny, concentric, and multispiral. Foot short, wide, rounded posteriorly and bilobed anteriorly, the lobes forming into finger-like processes. Rostrum and cephalic tentacles long. Eyes sessile and at the inner base of the tentacles. Gill external and feather-like, sometimes extended from the left side over the back and shell during locomotion. A long, slender pallial tentacle is also visible on the right side. Hermaphroditic, with long, slender, external penis and with female opening on right side between right gill and rectum. The radula is taenioglossate (formula 3-1-3) and the jaw is single and covered with small scales.

Valvatidae contains only 1 Recent genus, viz., *Valvata* Müller. Three extinct genera are also placed (Wenz, 1939: 508) in Valvatidae and 1 of these (*Orygoceras*, Upper Miocene to Lower Pliocene) has an entirely uncoiled and nearly straight shell. Geologic age: Carboniferous (?) or Jurassic to Recent.

Key to the species and subspecies of Valvatidae

1. Body whorl with spiral carinae or spiral angulations or both, which together total 3 in number . . . . *Valvata tricarinata* (p 234, Pl. 11, Fig. 7; Pl. 20, Figs. 4–6)
   Body whorl without spiral carinae or spiral angulations 2
2. Body whorl loosely coiled, i.e., peripherally detached from penultimate whorl; Western Ontario and vicinity . . . . *Valvata sincera ontariensis* (p 225, Pl. 11, Figs. 8, 9; Pl. 20, Fig. 2)
   Body whorl appressed to penultimate whorl 3
3. Collabral striae medium to widely spaced and coarse; umbilicus medium-sized; mainly boreal in distribution . . . . *Valvata sincera sincera* (p 222, Pl. 20, Fig. 1)
   Collabral striae closely spaced and fine; umbilicus wide; arctic and subarctic in distribution . . . . *Valvata sincera helicoidea* (p 229, Pl. 11, Figs. 4–6; Pl. 20, Fig. 3)

Genus *Valvata* Müller

Valvata O. F. Müller, 1774: *Vermium terrestrium et fluviatilium* (etc.), *2*: 198. Type species: *Valvata cristata* Müller, by monotypy. *Valvata* Müller has been placed on the Official List of Generic Names in Zoology (Name No. 838) by Opinion 335 of the International Commission on Zoological Nomenclature, 1955. Pending publication of the *Treatise on Invertebrate Paleontology*, vol. J, see Dall (1905: 120) for generic synonymy.

A brief description of the shell and soft part morphology of *Valvata* is given above under Family Valvatidae. See also Fretter & Graham (1962: 394).

Cleland (1954) has described the anatomy of the European *Valvata piscinalis* in considerable detail. She was unable to decide whether or not self-fertilization occurs, but the presence of a large penis implies that cross-fertilization is usual. Nevertheless, since the single duct from

the hermaphroditic organ leads both to the vas deferens and the oviduct, occasional self-fertilization appears probable.

Heard (1963c) has reviewed the literature on reproduction in *Valvata* and has recorded new observations on North American species. Reproduction occurs from late spring to late summer and, in the European *V. piscinalis*, 3 separate periods of migration into shallow water take place during which egg masses are deposited on aquatic plants. *Valvata* egg capsules are spherical and contain varying numbers of eggs (1 to 60) depending on the species. Developing embryos are green in most populations but after hatching that colour persists only in the digestive gland.

About 15 Recent species are known from North America, Europe, Asia, and Africa. Geologic range: Carboniferous (?) or Jurassic to Recent.

Valvata sincera sincera Say
Plate 20, Fig. 1; Map 42.

Valvata sincera Say, 1824: *Major Long's Second Exped. to the source of St. Peter's River* [etc.]. *2* (Appendix): 264, pl. 15: 11 (Binney reprint, 1858: 130). Type locality: " North-west Territory [United States]."

Valvata striata Lewis, 1856: *Proc. Acad. natr. Sci. Philad., 8*: 360. Type locality: " Little Lakes, New York."

Valvata lewisi Currier, 1868: *Kent. Sci. Inst., Misc. Publ. No. 1*, p 9. New name for *V. striata* Lewis, non Philippi, 1836.

Valvata (*sincera* var?) *nylanderi* Dall, 1905: *Land and fresh water mollusks of Alaska and Adjoining Regions*. Harriman Alaska Exped., *13*: 122. Type locality: " Aroostook County, Maine."

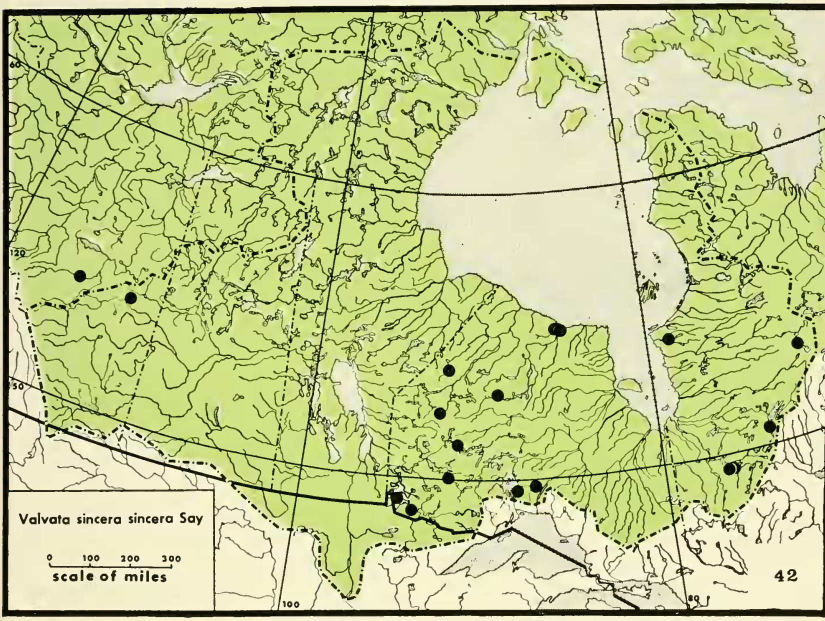
Diagnosis: Shell up to about 1/5 inch wide, conispiral, of moderate elevation, with a medium-sized umbilicus, widely-spaced collabral threads or lamellae which, in many specimens, are elevated and blade-like.

Description: " Shell subglobose-conic; whorls nearly four, accurately rounded, finely and regularly wrinkled across; aperture not interrupted by the penultimate whorl nor appressed to it, but merely in contact with it, the labrum not diminished in thickness at the point of contact; umbilicus large, exhibiting the volutions. Breadth less than one-fifth of an inch...It is very similar to the *tricarinata*, nobis, but is destitute of carinated lines, and the umbilicus is rather larger; it differs from the *obtusa* of Europe, also, in the much greater magnitude of the umbilicus." (Say, 1824).

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Stream 3½ mi E of Finland, Ont.					
Height (H), mm	15	1·6 —3·2	2·66	—	—
Diameter (D), mm	15	2·6 —4·9	3·94	—	—
H/D	15	0·54—0·76	0·689	0·021	0·081
Umbilicus diameter (Du)	15	0·5 —1·5	1·01	—	—
Du/D	15	0·17— 0·31	0·256	0·010	0·041
Sculpture Code*	15	3·0	3·00	0·00	0·00
Whorls	15	3·5 — 4·0	3·87	—	—

* See " Remarks on Coding."



Records:

Numerical notations (3–3, 3–2, etc.) indicate sculpturing and spire elevation. See "Remarks on Coding" below.

Eastern James Bay drainage area. Roggan River system: Middle Fork, Roggan River, 73 mi SSW of Poste de la Baleine (Great Whale River), Que. (3–2) (this survey). Fort George River system: Nitchequon, Que. (53°N, 70°30′W) (3–3) (1962, R. Goodland and W. K. W. Baldwin!). Rupert River system: Rivière à la Perche, 48 mi NE of Chibougamau, Que. (3–2) (this survey). Nottaway River system: O'Sullivan River, ½ mi N of Miquelon, Que. (3–2). Small river 10 mi ENE of Miquelon (3–2) (both this survey).

Albany River system. Lake 3 mi N of Geraldton, Ont. (3–3). Small pond near Orient Bay, Lake Nipigon, 20 mi S of Beardmore, Ont. (3–2) (both this survey). Head of Lake St. Joseph, Ont. (3–2) (1905, W. McInnes!).

Winisk River system. Wunnummin Lake (52°35′N, 92°38′W) (3–3) (1962, Ont. Dept. Lands and Forests!). Small ponds in marsh, 6 mi E of Winisk, Ont. ([2–3]–2) (this survey).

Severn River system. MacDowell Lake, Ont. (53°14′N, 90°47′W) (3–3) (this survey). Sachigo Lake, Ont. (53°49′N, 92°08′W) (3–2) (1964, Ont. Dept. Lands and Forests!).

Winnipeg River system. Kennedy Island, Lake of the Woods, Ont. (Baker, 1939b: 91). Stream 3½ mi E of Finland, Ont. (3–3). Inlet of small lake 3 mi W of Patricia, Ont. (3–2). Pelican Lake, Sioux Lookout, Ont. (3–2) (all this survey).

Saskatchewan River system. Caché Lake, 2 mi W of Spedden, Alta. (3–2), 1 specimen; (1–2), 15 specimens (this survey).

Athabasca River system. Inlet of Horn Lake, 10 mi SW of Whitecourt, Alta. (3–2) (this survey).

Distribution: Maine to Newfoundland and northern Quebec, west to Minnesota and Alberta. Some isolated populations live also in northern Ontario and numerous morphologically intermediate populations occur in the zone of contact with *Valvata sincera helicoidea*. See "Remarks".

Biology and Ecology: *Valvata sincera* was found at 13 localities during this survey,

as follows: 2 large lakes, 3 small lakes, 1 permanent pond (closely connected with a large lake), 1 large lake outlet (near the lake), 2 large rivers (over 100 feet wide), 1 river about 25 feet wide, 2 small streams in swamps, and 1 in a muskeg pool. Except for the Roggan River locality where the substrate was sand, all substrates were of mud with or without coarser sediments or rocks or both. Submersed vegetation was present but of variable density at each locality. In the lotic habitats current was slow to imperceptible.

Baker (1928a: 23) has recorded this species as chiefly in lakes and, in Lake Michigan and Lake Superior, in deep water. Present observations confirm its presence in large lakes and show that in the northern part of its range it also occurs in small water bodies, as do other presumably cold-stenothermal species.

The radula of *Valvata sincera* (*s. str.*) has been figured and described by Baker (1928a: 26). Its cusp formula is 15-1-15 (central), 10-1-15, 9-1-30, and 11-1-30. The jaw is described (loc. cit.) as covered with very small plates "much finer than in *tricarinata* and slightly finer than in *lewisi* [=*V. sincera* (*s. str.*)]" which overlap horizontally and vertically. Limited observations (Heard, 1963c: 66) indicate that each egg mass contains only a few (about 2 to 4) eggs and that hatching occurs quickly (about 5 to 8 days).

Remarks on Coding: The sculpture code used for the *Valvata sincera* group is: 0, smooth; 1, collabral striae, riblets, or lamellae close together (i.e., averaging more than 13 per mm on the body whorl); 2, moderately separated (i.e., averaging 9 to 13); 3, far apart (i.e., averaging fewer than 9). The spire elevation code is: 1, spire depressed and flat or nearly flat; 2, spire slightly elevated; 3, spire well elevated. For example (3-2) would indicate that all specimens in the lot have widely-spaced collabral sculpture and moderately elevated spires. Furthermore ([1-2]-3) would mean that specimens with fine collabral sculpture predominate but that specimens with moderately coarse sculpture were also present and that all specimens have high spires. The same representative specimens were used consistently as standards for comparison. Only populations in which all or most individuals have collabral sculpture of code value 3 were here considered as *V. sincera* (*s. str.*)

Remarks on Synonyms and Relationships: *Valvata sincera* exhibits little shell variation within most populations and rather extensive variation within others. Differences between populations are often great, however, and finely-ribbed (code 1) populations may occur in lakes which are adjacent to other lakes containing coarsely-ribbed (code 3) populations. Map 42 illustrates this point. Spire height also shows some inconsistencies in geographic pattern and loose coiling is not entirely restricted to one region.

Some morphologic-geographic trends *are* indicated, however (see Map 42). Coarse collabral sculpture is found most frequently in populations of the southern Canadian Interior Basin and in other populations farther south (*Valvata sincera sincera*). Loose coiling occurs, but only rarely, in "normal" populations at many localities but is expressed in all individuals of *V. sincera* (*s. lat.*) which live in 1 large area north of Lake Superior (see *V. s. ontariensis*). Similarly, flattened shells with fine sculpturing occur to a limited extent throughout the whole region but occur relatively consistently only in the central and northern parts of the research area (see *V. s. helicoidea*).

On morphological and geographical grounds 3 subspecies are therefore

considered valid, viz., *V. sincera* (*s. str.*), *V. s. ontariensis* and *V. s. helicoidea.*

The flattened, northern subspecies, discussed below, has been referred to as *Valvata lewisi* by previous authors. However, the only subspecies which occurs in the type region, Little Lakes, New York State, or in the vicinity of Grattan, Michigan, which was selected as type locality by Baker (1964a: 169), is *V. sincera* (*s. str.*). *V. lewisi* is a relatively smooth variant of *V. sincera* (*s. str.*) and it must be considered a biological synonym of that taxon.

Valvata sincera "*nylanderi*" (Pl. 20, Fig. 1) is an extreme morph but of an opposite kind. Its striations are strengthened and expanded to form sharp, blade-like periostracal lamellae. It also occurs in scattered populations in the region occupied by *V. sincera* (*s. str.*) and is not, therefore, entitled to taxonomic distinction. The periostracal lamellae are easily worn off and are best visible on fresh specimens.

The status of *Valvata sincera danielsi* Walker cannot be decided from available material but it is probably a valid taxon. It has been described as larger and proportionately higher than *V. sincera* (*s. str.*) and occurs in Pleistocene deposits in Wisconsin, Illinois, and Ontario and as living populations only in Minnesota. It is not known from the Canadian Interior Basin.

Valvata sincera ontariensis Baker
Plate 11, Figs. 8, 9; Plate 20, Fig. 2; Map 43

Valvata lewisi ontariensis Baker, 1931: *Nautilus*, *44*(4): 119. Type locality: "Shakespeare Island Lake [Shakespeare Island, Lake Nipigon], Ontario, Canada."

Valvata lewisi mccolli La Rocque, 1932: *Can. Field-Naturalist*, *46*(9): 199, text figs. Type locality: "Shallow Lake, Grey Co., Ont., in marl of late Wisconsin age (Pleistocene)."

Diagnosis: Shell up to about 1/5 inch wide, conispiral, with body whorl detached and loosely-coiled, and with widely-spaced, raised, blade-like collabral lamellae.

Description: Shell similar to *Valvata sincera* (*s. str.*) except that the body whorl, and in some specimens also the distal half of the penultimate whorl, are not peripherally attached to the preceeding whorl. The uncoiled portion is deflected downward and outward to the extent that near the aperture the space between the penultimate whorl and the body whorl is approximately twice the body whorl diameter. The collabral striae are prominently raised and widely separated, much as in *V. sincera* "*nylanderi.*"

Measurements :

Height, mm	Diameter, mm	H/D	No. of Whorls	No. of Whorls Loosely Coiled
"Kawinogans River" [Crow River], Ont.				
2·3	3·5	0·66	3·2	0·8
2·2	3·4	0·65	3·2	1·0
2·2	3·1	0·71	3·0	1·0
2·1	2·9	0·72	2·8	1·0
Klotz Lake, 30 mi E of Longlac, Ont.				
4·4	4·7	0·94	3·2	0·8
3·2	4·1	0·78	3·2	1·0
2·9	3·5	0·83	3·2	1·0
2·4	3·0	0·80	3·0	1·0
2·0	2·9	0·66	2·8	0·8

PLATE 20. *Valvata*

FIG. 1. *Valvata sincera sincera*, stream near Finland, Ontario (NMC 19555, 4·7 mm), ... p 222.

FIG. 2. *Valvata sincera ontariensis*, Klotz Lake, near Longlac, Ontario (NMC 14821, 5·6 mm) . . . . p 225.

FIG. 3. *Valvata sincera helicoidea*, Ennadai Lake, Northwest Territories (NMC 40126, 5·6 mm). . . . . p 229.

FIG. 4. *Valvata tricarinata* (1-0-1 morph), Lower Red Lake, Minnesota (NMC 32000, 5·3 mm), ... p 234.

FIG. 5. *Valvata tricarinata* (reduced carinae), Attawapiskat River, near Attawapiskat, Ontario (NMC 45820, 4·7 mm), ... p 234.

FIG. 6. *Valvata tricarinata* (fully carinate), Klotz Lake, near Longlac, Ontario (NMC 19119, 3·6 mm), ... p 234.

1

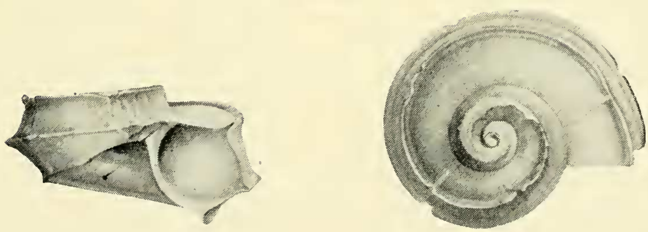
2

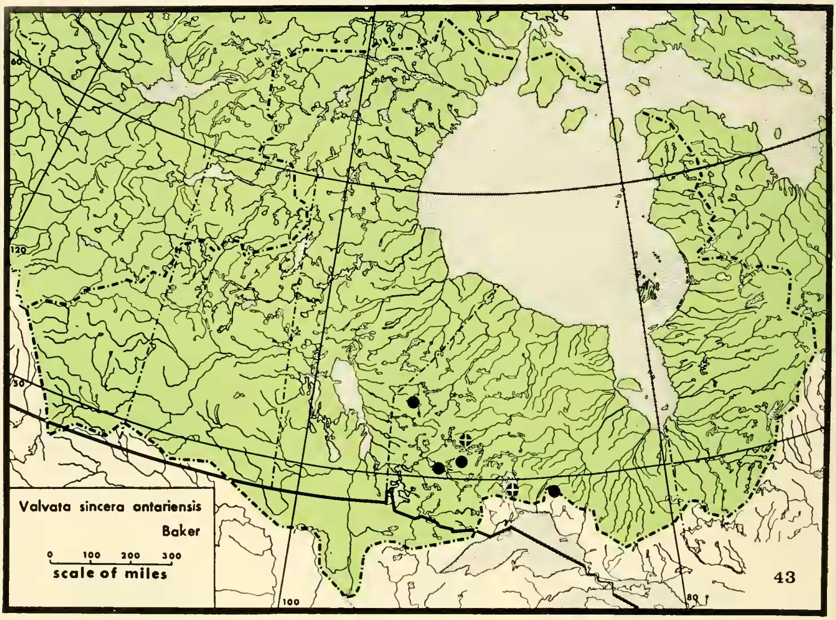
3

4

5

6





Records:

Attawapiskat River system. "Kawinogans River" [Crow River], Ont. (1904, W. Mc Innes!).
Albany River system. Shakespeare Island Lake, Shakespeare Island, Lake Nipigon, Ont. (type locality of "*Valvata lewisi ontariensis*") (Baker, 1931: 119). Kimmewin Lake, north of Drayton [Township] Ont. (Baker, 1931: 120). Lac Seul, Ont. (1919, F. W. Waugh!). Klotz Lake, 30 mi E of Longlac, Ont. (this survey).
Severn River system. Deer Lake, Deer Lake, Ont. (this survey).

Distribution: Northwestern Ontario in the region north of Lake Superior drained by the headwaters of the Attawapiskat, Albany and Severn River systems.

Biology and Ecology: During this survey *Valvata sincera ontariensis* was collected only in 2 large lakes, Klotz Lake and Deer Lake. All other records except "Kawinogans River" are also from large lakes. In Klotz Lake it occurred in depths of 3 to 28 feet, in shallow water principally among horsetails and in deeper water it was found where no vegetation was growing. Muddy sand or mud characterized all habitats. The Deer Lake specimens occurred in a similar situation, i.e., among horsetails, on a sandy mud bottom, and in 3 to 4 feet of water.

Klotz Lake was visited on 4 occasions during 3 field seasons. Relative abundance of *Valvata sincera ontariensis* varied widely. It constituted only 1·7% of the 350 snails collected on June 2, 1965 (dredge used in 6 to 28 feet of water), 5·7% of the 35 snails collected on June 26, 1965 (dredge, 8 to 12 feet), 0·14% of the 1,400 snails collected on

July 18, 1961 (dip net, 3 to 4 feet), and 4·0% of the 100 snails collected on August 3, 1960 (dip net, 4 to 6 feet). At Deer Lake it constituted 14% of the 14 snails collected on August 11, 1967 (dip net, 3 to 4 feet).

The species found to be most consistently associated with *Valvata sincera ontariensis* are *Gyraulus parvus*, *Helisoma campanulatum*, *Valvata tricarinata* and *Amnicola limosa*.

Living specimens from Klotz Lake were observed to move rather slowly. The shell is carried at an angle of about 45°. The animal moves forward with the shell stationary, hitches the shell forward suddenly, and then repeats, thus transporting the shell in a series of slow jerks.

Remarks: The status of *Valvata sincera ontariensis* as a valid subspecies has been open to some question because loosely-coiled *V. sincera* occur also (rarely) in some apparently normal populations. In Klotz Lake, however, and presumably in other lakes in northwestern Ontario the populations are uniform and *all* specimens of the *V. sincera* group are loosely coiled.

Two juvenile specimens morphologically identical with this subspecies were also collected in a tributary of the Souris River, 2 mi S of Weyburn, Sask. (this survey). No " normal " specimens of *Valvata sincera* were found there but the data are insufficient to establish whether or not this is a " pure " population of loosely-coiled individuals. The same restriction applies to the Deer Lake sample. Pleistocene fossils and empty, worn shells which may be Pleistocene have also been found in Shallow Lake, Grey County, Ont. (La Rocque, 1932) and in a lake NW of Cormorant Lake, Man. (1906, W. McInnes!) but it is not known whether these represented " pure " loosely coiled populations or if the specimens had been selected from normal populations which included a few loosely-coiled individuals.

Valvata sincera helicoidea Dall
Plate 11, Figs. 4-6; Plate 20,
Fig. 3; Map 44.

Valvata lewisi var. *helicoidea* Dall, 1905: *Land and fresh water mollusks of Alaska and adjoining Regions*. Harriman Alaska Exped., *13*: 125, pl. 11: 1–2 (as " *Valvata helicoidea* Dall "). Type locality not specified but 4 localities are cited in Alaska, British Columbia and Yukon Territory.

Diagnosis: Shell about $\frac{1}{4}$ inch wide, depressed, conispiral, with wide umbilicus, and with fine to obsolete collabral striae.

Description: Shell up to 5 mm high, about $1\frac{1}{3}$ to $1\frac{2}{3}$ wider than high, depressed, of medium thickness, whorls round and without spiral keels or angulations, and brownish. Nuclear whorl planorboid and with fine spiral striae. Spire depressed, nearly flat or slightly elevated. Whorls about $3\frac{1}{2}$-4, round in cross-section, rapidly increasing in diameter, and adnate to the previous whorl throughout a narrow zone only. Aperture round and lip thin and continuous. Umbilicus wide, deep, and exhibiting about half of the under surfaces of the penultimate and all previous whorls. Sculpture typically consisting of irregularly spaced growth rests and of fine crowded collabral riblets " like the winding of threads on a spool " (Dall, 1905: 123). Riblets varying from absent (surface smooth) to coarse and rather widely spaced. Spiral striae occur rarely. Collabral sculpture resides principally in the periostracum which is of only moderate thickness but firmly adherent and chestnut, reddish-brown, or yellowish-tan in colour. Operculum round, horny, multispiral, with about 10 turns, of medium thickness, slightly concave, and neatly filling the aperture.

Measurements :

Feature	N	Range	Mean	S.E.$_M$	S.D.
Caché Lake, 2 mi W of Spedden, Alta.					
Height (H), mm	15	1·8 —2·8	2·17	—	—
Diameter (D), mm	15	2·5 —4·6	3·02	—	—
H/D	15	0·61—0·82	0·724	0·015	0·059
Umbilicus diameter (Du)	15	0·6 —1·2	0·78	—	—
Du/D	15	0·22—0·29	0·260	0·005	0·022
Sculpture Code*	15	0·0 —3·0	1·13	0·22	0·83
Whorls	15	3·0 —4·0	3·57	—	—
Lac la Ronge, Sask.					
Height (H), mm	15	2·8 —3·7	3·30	—	—
Diameter (D), mm	15	3·7 —5·3	4·45	—	—
H/D	15	0·68—0·77	0·743	0·016	0·062
Umbilicus diameter (Du)	15	0·8 —1·2	1·93	—	—
Du/D	15	0·21—0·30	0·246	0·007	0·027
Sculpture Code*	15	1·0	1·0	0·0	0·0
Whorls	15	4·0	4·0	—	—
Opachuanau Lake, Man. (56°44′N, 99°37′W).					
Height (H), mm	15	3·6 —5·2	4·24	—	—
Diameter (D), mm	15	4·8 —7·0	5·35	—	—
H/D	15	0·71—0·85	0·793	0·011	0·044
Umbilicus diameter (Du)	15	1·0 —1·8	1·13	—	—
Du/D	15	0·17—0·26	0·210	0·005	0·023
Sculpture Code*	15	1·0	1·0	0·0	0·0
Whorls	15	4·0	4·0	—	—
Aberdeen Lake, N.W.T. (64°38′N, 100°00′W).					
Height (H), mm	15	2·1 —3·2	2·57	—	—
Diameter (D), mm	15	3·9 —5·1	4·62	—	—
H/D	15	0·45—0·63	0·557	0·012	0·047
Umbilicus diameter (Du)	15	1·0 —2·1	1·46	—	—
Du/D	15	0·26—0·43	0·315	0·011	0·042
Sculpture Code*	15	1·0	1·0	0·0	0·0
Whorls	15	4·0	4·0	—	—

* See " Remarks on Coding " under *Valvata sincera* (*s. str.*) for explanation.

Records:

See "Remarks" under *Valvata sincera* (*s. str.*) for explanation of numerical coding of sculpturing and spire elevation.

Ungava Bay drainage area, Quebec. Lac Áigneau (57°08'—57°13'N, 70°35'W) (1–2) (1955, D. R. Oliver!). Fort Chimo (1–2) (1896, W. Spreadborough!).

Eastern Hudson Bay and eastern James Bay drainage areas, Que. Lake 2 mi N of Inoucdjouac (Port Harrison) (1–2). River lake, Nastapoka River, 2 mi E of Nastapoka Sound (2–?, worn). Pond near Clearwater River, ¾ mi E of Richmond Gulf (2–2). Burton Lake, N side near middle of lake, 33 mi SSW of Poste de la Baleine (Great Whale River) (2–3). Fort George River (1–2) (all this survey).

Nottaway River system, Que. Waswanipi River, 22 mi NE of Demaraisville (1–1) (this survey).

Moose River system, Ont. Pond 6 mi S of Matheson (1–2) (this survey). Swamp at Moose factory (2–2) (*ca.* 1951, E. B. Chamberlin).

Albany River system, Ont. Lake Nipigon (2-[2–3]) (some approaching *V. s. ontariensis*) (1884. J. Macoun!). Bamaji Lake (51°10'N, 91°25'W) ([1–2]–2) (this survey). Lake St. Joseph (2–2) (1905, W. McInnes!). Yellow Creek, near Fort Albany (2–2). Ox-bow lake at Devil's Gut, south of Albany Island. Marsh, south side of Albany Island, 2 mi W of east end (1–2). Mouth of Albany River, east end of Albany Island, in tidewater ([1–2]–2) (all this survey).

Attawapiskat River system, Ont. Attawapiskat Lake (52°18'N, 87°54'W) (2–1) (1961, Ont. Dept. Lands and Forests!) Monument Channel at portage, 20 mi W of Attawapiskat ([1–3]–[2–3]). Attawapiskat River, ½ mi W of Attawapiskat ([1–2]–2). Muskeg near north bank of Attawapiskat River, 1 mi E of Attawapiskat ([1–2]–2) (all this survey).

Sutton River system, Ont. Hawley Lake (54°30'N, 84°39'W) (1–2) (1961, Ont. Dept. Lands and Forests!).

Severn River system, Ont. Severn Lake, south end (2–2) (this survey). Magiss Lake (52°59'N, 91°40'W) (2–1) (1963, Ont. Dept. Lands and Forests!).

Hayes River system. Red Sucker Lake, Man. (54°10'N, 93°57'W) (2–3). Knee Lake, northern narrows, Man. (55°04'N, 94°45'W) ([0–2]–2) (both this survey).

Saskatchewan River system. South Saskatchewan River system: Inlet of Third Vermilion Lake, Banff, Alta. (1–2) (this survey). Sylvan Lake, east end, Alta. (1–2) (1929, L. S. Russell!). North Saskatchewan River system: Wabamun Lake, Alta. (?–2, worn) (1926, L. S. Russell!). Bigstone Creek, 2 mi W of Spedden, Alta. (1–2 and 3–2). Halkett Lake, 20 mi S of Waskesiu Lake, Sask. (?–2) (all this survey). Saskatchewan River system: Root Lake, 19 mi N of The Pas, Man. (this survey). Cormorant Lake, Man. (2–[2–3]) (1906, W. McInnes!).

Nelson River system. Lake Winnipeg, 20 mi S of Gimli, Man. (?–2). Lake, 27 mi E of Simonhouse, Man. (1–2) (both this survey).

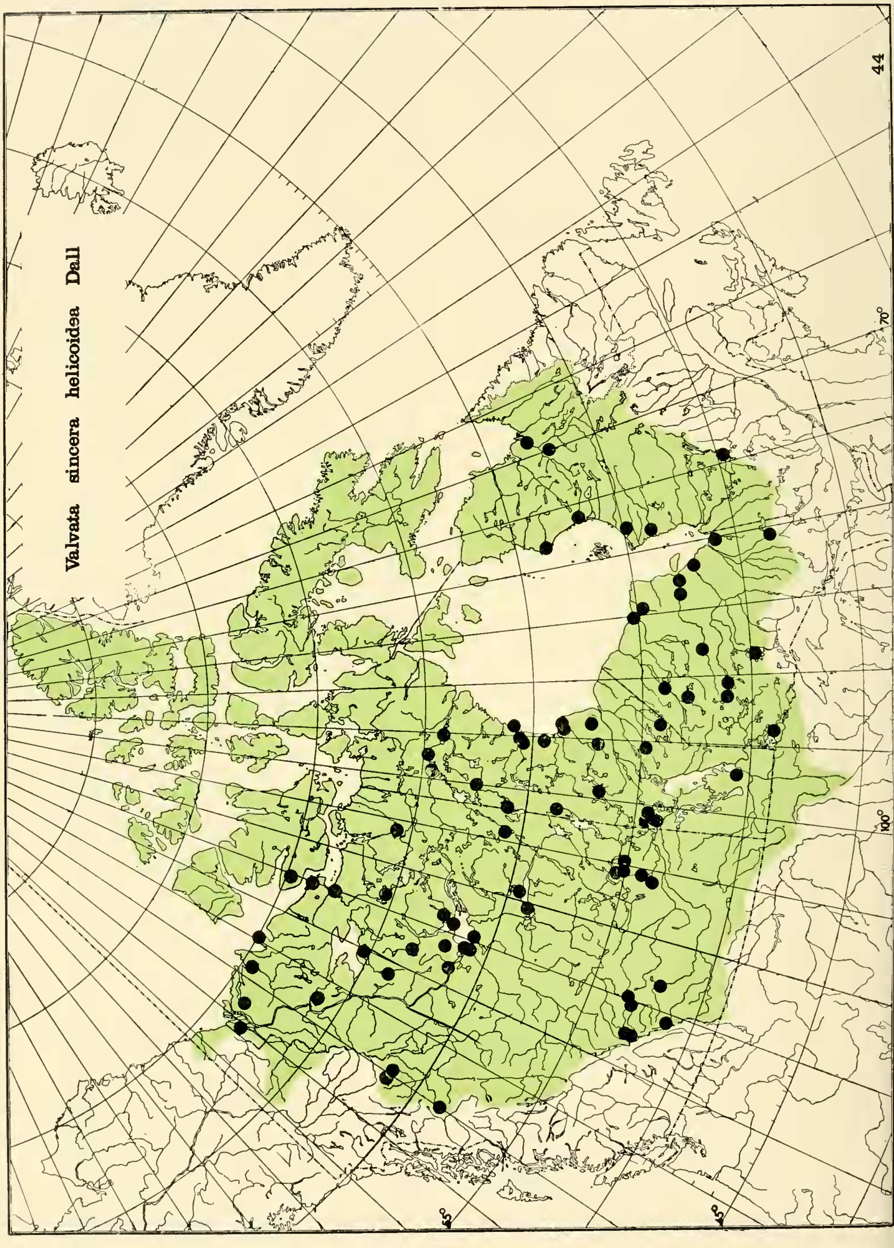
Owl River system. Owl Lake, Man. (56°22'N, 94°35'W) (1–2) (this survey).

Churchill River system. Montreal Lake, south end, 16 mi N of Waskesiu Lake, Sask. (?–3) (this survey). Lac la Ronge, Sask. (1–[2–3]) (1934, Univ. Sask.!). Stream 4 mi N of La Ronge, Sask. ([2–3]–[1–2]). Lynx Lake, 29 mi N of La Ronge (2–2). Brochet Lake, east end, Man. (58°35'N, 101°35'W) (0–2). Opachuanau Lake, Man. (56°44'N, 99°37'W) (1–3). Recluse Lake, Man. (56°55'N, 95°45'W) ([1–2]–[2–3]). Goose Creek, 7 mi S of Churchill, Man. (1–2) (all this survey).

Western Hudson Bay drainage area. Caribou River system: Long Lake, east end, Man. (59°24'N, 93°18'W) (1–2) (this survey). Thlewiaza River system: Unnamed lake in Thlewiaza River, N.W.T. (60°23'N, 95°45'W) (1–1) (this survey). Tha-Anne River system: Hyde Lake, N.W.T. (60°45'N, 95°22'W) (1–[1–2]) (1959, Fish. Res. Bd.!). McConnell River system: McConnell River, 18 mi S of Eskimo Point, N.W.T. (1–[1–2]) (1960, S. D. MacDonald!). Wilson River system: Maze Lake, N.W.T. (62°24'N, 93°27'W) (1–1) (1959, Fish. Res. Bd.!).

Thelon River drainage area, N.W.T. Kazan River system: Ennadai Lake, southwest end (60°45'N, 101°46'W) (1–1). Angikuni Lake (62°15'N, 100°00'W) (1–1) (both this survey). Dubawnt River system: Wholdaia Lake, (60°45'N, 118°08'W) (1–1) (1959, Fish. Res. Bd.!). Thelon River system: Whitefish Lake (62°36'N, 106°45'W) (1–1) (1959, Fish. Res. Bd.!). Aberdeen Lake, 12 localities (1–1) (1961, Elizabeth Macpherson!). Schultz Lake (64°45'N, 97°30'W) (1–[1–2]) (1958, Fish. Res. Bd.!). Baker Lake, 12 mi S of Baker Lake settlement (1–1) (1962, W. C. Donahue, E. W. Smith!).

Northern Arctic drainage area, N.W.T. Back River system: Redrock Lake (65°28'N, 114°10'W) (1–[1–2]) (1959, W. B. Scott!). Beechy Lake (65°12'30"N, 106°28'W) (1–1) (1959 Fish. Res. Bd.!). Coppermine River system: Vaillant Lake (66°12'N, 114°29'W) (1–1) (1959, Fish. Res. Bd.!). Bloody Falls, Coppermine River (67°45'N, 115°21'W) (1–[1–2]) (1957,


Valvata sincera helicoidea Dall
44
70°
100°

Fish. Res. Bd.!). Coastal drainage area: Creek, Bernard Harbour (1–1) (1916, F. Johansen!). Lake, Wollaston Peninsula, Victoria Island (1–2) (1915, D. Jenness!). Lake, Cape Parry (69°27′N, 124°30′W) (1–1) (1962, G. Abrahamson!). Anderson River (1–[1–2]) (1958, Fish. Res. Bd.!). Camp stream, Husky Lakes (1–1, some spirally striate) (1955, Fish. Res. Bd.!).

Mackenzie River system. Athabasca River system: Moab Lake ([1–2]–2), Patricia Lake (1–2), Pyramid Lake (1–2) (all 1954, Can. Wildlife Serv.!) and Leach Lake (1–2) (1964, R. W. Coleman!), Jasper National Park, Alta. Slave River system: Lake Athabasca, "The Willows" (1–2) and Camsell Portage (1–1) (both 1945, Univ..Sask!). Liard River system: Dease Lake, B.C. ([1–2]–[1–2]), with spiral striae (1962, S. D. MacDonald!). Frances Lake, Y.T. (1–1) (1887, G. M. Dawson!). North Toobally Lake, Y.T. (1–1) (1961, P. M. Youngman!). Great Bear Lake drainage area: Beaverlodge Lake (64°42′N, 118°12′W) (1–2) (1959, W. B. Scott!). Keller Lake, 7 m depth (64°00′N, 121°30′W) (1–[1–2]) (1962, Fish. Res. Bd.!). McVicar Arm, Great Bear Lake (1–1) (1964, Fish. Res. Bd.!). Mackenzie River system: Great Slave Lake, several localities (1–1 and 1–[1–2]). Lac la Martre (63°10′N, 117°20′W) (1–[1–2]) (1959, Fish. Res. Bd.!). Beaver Lake, 30 mi E of Pt. Providence (?–3, worn). Birch Lake, Horn River (1–[1–3]) (both 1921, E. J. Whittaker!). Mills Lake (1–[1–3]) (1917, E. M. Kindle!; 1919, E. J. Whittaker!). Lac à Jacques (66°10′N, 127°25′W) (1–[1–2]). Fossil Lake (66°17′N, 128°55′W) (1–[1–2]) (both 1962, Fish. Res. Bd.!). Mackenzie River, Aklavik (1–[1–2]) (1957, Fish. Res. Bd.!).

Distribution: Throughout the Canadian Interior Basin north to a line running from Ungava Bay to southern Victoria Island, south into the boreal forest region almost to the Great Lakes-St. Lawrence River drainage area and with some populations in western parkland localities, east to Labrador, and west to British Columbia and Alaska.

Biology and Ecology: Thirty-seven lots of *Valvata sincera helicoidea* were collected during this survey from differing habitats as follows: 15 are from large lakes, 6 from small lakes, 4 from permanent ponds, 10 from rivers of various widths (from 400 feet wide to 15 feet wide) and 2 from subarctic muskeg pools. Aquatic vegetation was present in all habitats but in various amounts; substrates were of all types with mud or sand predominating; and in lotic habitats current was moderate, slow, or not discernible.

In arctic lakes submersed aquatic vegetation is often absent in shallow water and *Valvata sincera helicoidea* is then also absent in that zone. At Aberdeen Lake, N.W.T., Mrs. Elizabeth Macpherson did not find that species in shallow water during late June to late July, 1961, but collected it frequently from the stomachs of whitefish. Nearly all Fisheries Research Board collections from other arctic lakes were also from whitefish. At Lac Aigneau, in Ungava, Dr. D. R. Oliver dredged it at several localities during the summer of 1955 from depths of 1·5 to 15 metres. In general it appears that *V. s. helicoidea* is eurytopic and eurybathic and is an abundant species in much of the Arctic and Subarctic wherever aquatic vegetation occurs.

Baker (1928a: 27-29) has described the jaw and radula of "*Valvata lewisi helicoidea*" as the same as that in "*V. lewisi*". Specimens of the latter, presumably from Lake Butte des Morts, Wisconsin, had scales on the jaw slightly larger than "*sincera*" and a radula cusp formula of 9-1-9, 9-1-13, 10-1-18, 23. The central tooth was 55 microns wide.

The results of examination of radulae from specimens collected in Moab Lake, Jasper National Park, Alta. and Vaillant Lake, N.W.T., are given below. Although many more specimens need to be studied to determine the extent of radula variation, it is already clear that the number of cusps on individual teeth and the width of the central teeth are widely variable.

Locality	Shell diameter mm	Radula cusp formula	Width of central tooth (microns) *
Moab Lake	4·3	12–1–12, 7–1–12, 8–1–18, 9–1–12	78
,, ,,	? (broken)	14–1–14, 7–1–11, 9–1–20, 11–1–18	75
Vaillant Lake	5·1	12–1–12, 10–1–13, 12–1–18, 28	84
,, ,,	4·9	13–1–13, 12–1–14, 11–1–17, 12–1–24	90

* An adult *Valvata tricarinata* from Abitibi River, 17 mi N of Cochrane, Ont. was also examined for radular characters. Its central tooth was only 54 microns wide.

It is also clear that the distinct but parallel species groups proposed by Walker and elaborated by Baker (1928a: 30) (Group 1: *Valvata tricarinata* plus *V. sincera*, central tooth 70 microns wide; Group 2: *V. bicarinata*, "*V. lewisi*", *V. l. helicoidea*, etc., central tooth 45 to 55 microns wide) are partly based on the incorrect belief that the width of the central radula tooth is constant. In addition, the probability of gene exchange between *V. sincera* (Group 1) and V. "*lewisi helicoidea*" (Group 2) is great, as demonstrated by the present study. The groups of *Valvata* suggested by Walker are therefore considered invalid.

Valvata tricarinata (Say)

Plate 11, Fig. 7; Plate 20, Figs. 4-6; Map 45.

Cyclostoma tricarinata Say, 1817: *J. Acad. natr. Sci. Philad.*, *1*: 13 (Binney reprint 1858: 59). Type locality: "Inhabits the river Delaware."

Valvata tricarinata var. *simplex* Gould, 1841: *Rept. on the Invertebrata of Mass.*, p 226. Type locality: "Vermont."

Valvata unicarinata DeKay, 1843: *Zool. New York*, *5* (Mollusca): 119, pl. 6: 129. Type locality: "Lake Champlain [and] Erie Canal [New York]."

Valvata tricarinata infracarinata Vanatta, 1915: Two new varieties of *Valvata*. *Nautilus*, *28*(9): 104, text figs. 1, 2. Type locality: "White Pond, New Jersey."

Valvata tricarinata basalis Vanatta, 1915: Op. cit., p 105, text figs. 3, 4. Type locality: "Hudson River, New York."

Valvata tricarinata perconfusa Walker, 1917: *Nautilus*, *31*(1): 36. Type locality not specified. (New name for *V. t.* var. *confusa* Walker, 1902; non *V. confusa* Westerlund, 1897).

Valvata tricarinata mediocarinata Baker, 1928: *Fresh Water Mollusca of Wisconsin*, *1*: 17, pl. 1: 7. Type locality: "Lower Asylum Bay, Lake Winnebago."

Diagnosis: Shell up to about ¼ inch wide, spire short, body whorl with 3 strong, spiral carinae or spiral angulations and aperture round.

Description: Shell up to 5 mm high, wider than high, solid, spirally angled or carinate, and brownish to green. Nuclear whorl planorboid and with microscopic spiral striae. Whorls about 4, with 3 strong, evenly spaced spiral cords, 1 at the shoulder, 1 at the periphery, and 1 bounding the umbilicus. One or more of the cords may be reduced in varying degrees but the locus of each missing cord is discernible at least as a spiral angulation. The lowest (and often the middle) cord or angulation on the spire whorls is covered by the following whorl. Whorls flattened between carinae and sloping upward from upper carina to suture. Sutures distinct and impressed. Aperture round internally and angled externally by the carinations or angulations; lip continuous and adnate to the body whorl for only a short distance. Umbilicus round, funnel-shaped, and deep. Fine sculpture consisting of distinct, crowded growth lines and poorly defined spiral lines. Colour brownish, pea-green, or emerald green. Operculum round, horny, multispiral and with about 10 turns.

Measurements:

Carina strength is coded using the following approximate scale: 0, carina absent, area rounded; 1, carina absent, area angled (as in Pl. 20, Fig. 4); 2, carina present and moderately developed (Pl. 20, Fig. 5); 3, carina extremely well-developed (Pl. 20, Fig. 6). Intermediate values are indicated as 1·7, 2·4, etc.

Feature	N	Range	Mean	S.E.$_M$	S.D.
Minnedosa River, 11 mi NNE of Elphinstone, Man.					
Height (H), mm	15	2·5 —4·8	3·23	—	—
Diameter (D), mm	15	3·2 —5·3	4·17	—	—
H/D	15	0·65—0·91	0·783	0·018	0·072
Upper carina strength	15	2·5 —3·0	2·73	0·05	0·18
Middle carina strength	15	2·0 —3·0	2·53	0·08	0·31
Lower carina strength	15	2·0 —2·8	2·61	0·06	0·23
Whorls	15	3·0 —4·0	3·50	—	—
Traverse Lake, Brown's Valley, Minn.					
Height (H), mm	15	2·3 —5·1	3·71	—	—
Diameter (D), mm	15	3·0 —6·2	4·55	—	—
H/D	15	0·74—0·88	0·816	0·011	0·043
Upper carina strength	15	2·5 —3·0	2·97	0·03	0·13
Middle carina strength	15	2·0 —3·0	2·83	0·10	0·37
Lower carina strength	15	2·5 —3·0	2·97	0·03	0·13
Whorls	15	3·0 —4·0	3·67	—	—
Lower Red Lake, Minn., 1 mi S of outlet.					
Height (H), mm	15	2·8 —4·2	3·58	—	—
Diameter (D), mm	15	4·4 —5·2	4·75	—	—
H/D	15	0·62—0·84	0·754	0·013	0·053
Upper carina strength	15	1·0 —3·0	2·13	0·10	0·40
Middle carina strength	15	0·0 —3·0	0·87	0·18	0·69
Lower carina strength	15	1·0 —3·0	2·87	0·09	0·35
Whorls	15	3·0 —4·0	3·25	—	—
Monument Channel at portage, 20 mi W of Attawapiskat, Ont.					
Height (H), mm	15	1·5 —4·6	2·84	—	—
Diameter (D), mm	15	2·1 —5·3	3·69	—	—
H/D	15	0·67—0·88	0·764	0·018	0·070
Upper carina strength	15	2·0 —2·8	2·29	0·07	0·28
Middle carina strength	15	2·0 —2·5	2·07	0·05	0·18
Lower carina strength	15	2·0 —2·5	2·13	0·06	0·23
Whorls	15	2·0 —4·0	3·07	—	—

Records:

Code numbers indicate presence (1) or absence (0) of upper, middle, and lower carinae, respectively. See " Remarks ".

Eastern James Bay drainage areas. Eastmain River system: Eastmain River, Eastmain, Que. (1–0–1, 0–0–1, 0–0–0) (this survey). Rupert River system: Rivière à la Perche, 48 mi N of Chibougamau, Que. (1–1–1). Bordeleau River, 20 mi NE of Chibougamau, Que. (1–1–1) (both this survey).

Nottaway River system. Caché Lake, near Chibougamau, Que. (1–0–1). Waswanipi River, 22 mi N of Demaraisville, Que. (1–0–1, 1–0–0) (both this survey).

Harricanaw River system. Lac Dubuisson, 5 mi NW of Val d'Or, Que. (1–1–1) (this survey).

Moose River system. Duparquet River, 3 mi N of Rapide Danseur, Que. (1–1–1). Lillabelle Lake, 5 mi N of Cochrane, Ont. (1–1–1). Abitibi River, 17 mi N of Cochrane, Ont. (1–1–1, 1–0–1). Pond 6 mi S of Matheson, Ont. (0–0–0). Black River, Matheson (1–1–1). Wilson Lake, 1½ mi S of Nellie Lake, Ont. (1–1–1). Groundhog River, Fauquier, Ont. (1–1–1) (all this survey). Moose River, Moose Factory, Ont. (1–1–1) (1934, R. Louttit!), (1–0–1, 0–0–0) (this survey). Moose River estuary, Shipsands Island (1–0–1, 1–0–0) (1933, H. G. Richards!).

Albany River system, Ont. Lake Nipigon (1–1–1) (1884, J. Macoun!). Skunk River, 38 mi W of Hearst (1–1–1). Pagwachuan River, 70 mi W of Hearst (1–1–1). Klotz Lake, 30 mi E of Longlac, in 4 to 15 feet of water, (1–1–1, unusually flattened). Kenogamisis Lake, 7 mi SE of Geraldton (1–1–1). Hutchinson Lake, 5 mi N of Geraldton (1–1–1, 1–0–1). Medcalfe Lake, north end, 63 mi N of Savant Lake (1–1–1) (all this survey). Lake St. Joseph, (1–1–1) (1904, W. McInnes!). Bamaji Lake, at outlet (1–0–1) (1929, A. R. Cahn!). Albany River, 9 mi W of Fort Albany, Ont. (1–1–1, 1–0–1) and 7 mi W of Fort Albany (1–1–1, 1–0–1). Albany River estuary: small pond adjacent to Devil's Gut, south of Albany Island (0–0–0); marsh, south side of Albany Island (1–1–1, 0–0–0); edge of James Bay in tidewater, east end of Albany Island (1–0–1) (all this survey).

Attawapiskat River system. Small stream 4 mi W of Pickle Crow, Ont. (1–1–1) (this survey). Monument Channel at portage to Attawapiskat River, 20 mi W of Attawapiskat, Ont. (1–1–1, unusually tall spires). Monument Channel, 12 mi and 6 mi W of Attawapiskat (both 1–1–1). Attawapiskat River 17 mi (1–1–1), 6 mi (1–1–1, 1–0–1), and ½ mi (1–1–1) W of Attawapiskat, Ont. (all this survey).

Sutton River system. Sutton Lake, Ont. (1–1–1) (1901, D. B. Dowling!).

Winisk River system. Wapikopa Lake, Ont. (53°00′N, 87°57′W) (1–1–1) (1904, W. McInnes!). Shamattawa River, ½ mi and 1 mi S of Winisk River, about 22 mi S of Winisk, Ont. (both 1–1–1). Winisk River, 22 mi, 16, and 15 mi S of Winisk (all 1–1–1). Ponds in muskeg 6 mi E of Winisk and 1½ mi from Hudson Bay (1–1–1) (all this survey).

Shell Brook system. Lake at head of Shell Brook (55°20′N, 87°17′W), Ont. (1–1–1) (this survey).

Severn River system. Magiss Lake (52°59′N, 91°40′W) (1–1–1), Sakwaso Lake (53°01′N, 91°55′W) (1–1–1), Sandy Lake (53°02′N, 93°00′W) (1–1–1) and Sachigo Lake (53°49′N, 92°08′W) (1–1–1), Ont. (1962–64, Ont. Dept. Lands and Forests!).

Hayes River system. Knee Lake at Northern Narrows (55°04′N, 94°45′W), Man. (1–1–1) (this survey).

Winnipeg River system. Sturgeon River [Marchington River], 1 mi W of Superior Junction, Ont. (1–1–1) (this survey). Kimmewin Lake (1–0–1) and Botsford Lake (1–1–1), near Drayton, Ont., (both 1929, A. R. Cahn!). Off Lake outlet, 4 mi NE of Finland, Ont. Lake of the Woods, 2 mi W of Kenora, Ont. Empty shells dredged in 60 feet of water (1–1–1) (both this survey).

Brokenhead River system. Hazel Creek, 2 mi E of Hazel, Man. (1–1–1) (this survey).

Red River system. Traverse Lake, Brown's Valley, Minn. (1–1–1). Lower Red Lake, ½ mi S of outlet into Red Lake River, 40 mi NNW of Bemidji, Minn. (1–1–1, 1–0–1, 1–0–0). Red River, 2 mi NE of Drayton, N.D. (1–1–1). Rat River, 1½ mi S of La Rochelle, Man. (1–1–1). Souris River [Mouse River], Mouse River Park, 15 mi WNW of Mohall, N.D. (1–1–1) (all this survey). Lady Lake, Sask. (1–1–1) (1961, D. Buckle!). Shell River, Man. (1–0–1, 0–0–0), (1887, J. B. Tyrrell!). Qu'Appelle Lake, 4½ mi NW of Katepwa, Sask. (1–1–1) (this survey). Echo Lake, Sask. (1-1-1) (1964, D. Delorme!). Qu'Appelle River: at Pasqua Lake outlet, Echo Valley Prov. Park, Sask. (1–1–1) and 11 mi N of Whitewood, Sask. (1–1–1). Whitesand River, 9 mi ESE of Sheho, Sask. (1–1–1). Creek, outlet of Campbell Lake, 8 mi ENE of Erickson, Man. (1–1–1). Clear Lake, north shore 8 mi N of Wasagaming, Man. (1–1–1). Minnedosa River: 10 mi NNW of Minnedosa, Man. (1–1–1) and 11 mi NNE of Elphinstone, Man. (1–1–1) (all this survey).

Lake Manitoba-Lake Winnipegosis drainage area: Barrier Lake (1–1–1) and Kipabiskau Lake (1–1–1), Sask. (both 1964, D. Delorme!). Lake Manitoba: 7 mi W of Ashern, Man. (1–1–1), 7 mi N of Moosehorn, Man. (1–1–1), and 1 mi N of Narrows (1–1–1) (all 1964, Marcel Ouellet!).

Saskatchewan River system. South Saskatchewan River drainage area: Blindman River, 5 mi N of Red Deer, Alta. (1–1–1) (this survey). Red Deer River at mouth of Blindman River, Alta. (1–1–1) (1927, R. L. Rutherford!). Gull Lake, Alta. (1–1–1). Swift Current Creek, 3 mi N of Waldeck, Sask. (1–1–1) (both this survey). North Saskatchewan River drainage area: Wabamun Lake, Seba Beach, Alta. (1–1–1) (1926, L. S. Russell!). North Saskatchewan River at Horseshoe Bend, near Edmonton, Alta. (1–1–1) (1925, L. S. Russell!). Whitney Lake, 6 mi SE of Lindbergh, Alta. (1–1–1). Turtlelake River, Edam, Sask. (1–1–1). Jackfish Lake, Meota, Sask. (1–1–1). Halkett Lake, 20 mi S of Waskesiu Lake, Sask. (1–1–1) (all this survey). Saskatchewan River drainage area: Cormorant Lake, Man. (1–1–1) (1906, W. McInnes!). Root Lake, 19 mi N of The Pas, Man. (1–1–1) (this survey).

Nelson River system. Lake Winnipeg, 20 mi S of Gimli, Man. (1–1–1) (this survey). Playgreen Lake, Man. (1–1–1) (1878, R. Bell!). Lake 27 mi E of Simonhouse, Man. (1–1–1). Limestone Lake, east end, Man. (56°35′N, 96°00′W) (1–1–1, 0–0–0) (both this survey).

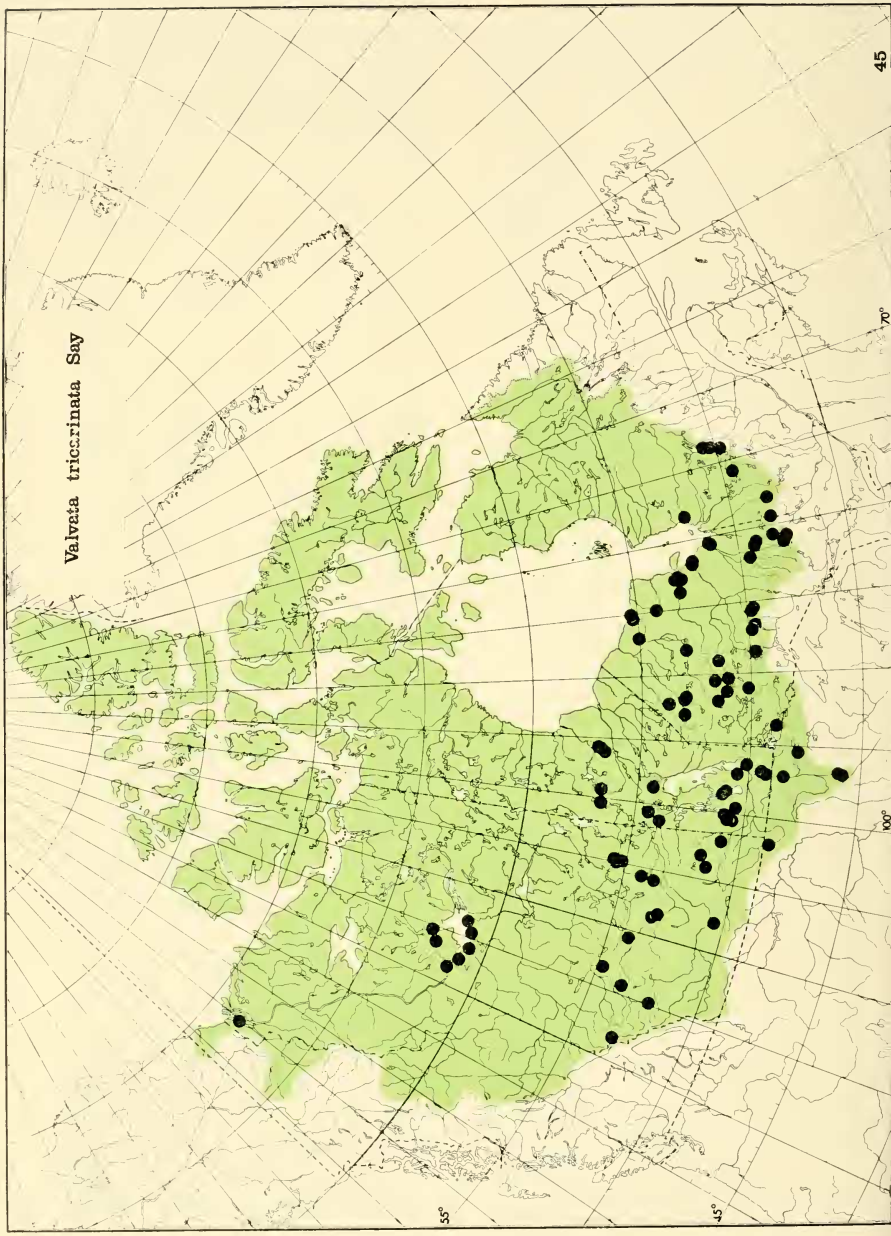
Churchill River system. Montreal Lake, south end, 16 mi N of Waskesiu Lake, Sask. (1–1–1) (this survey). Lac la Ronge, Sask., (from whitefish) (1–1–1) (1954, Univ. Sask.!). Waden Bay, Lac la Ronge, 17 mi N of La Ronge, Sask. (dredged, 18 feet), (1–1–1). Lynx Lake, 29 mi N of La Ronge (1–1–1). Eden Lake, at outlet, Man. (56°38′N, 100°15′W) (1–1–1). Opachuanau Lake, Man. (56°44′N, 99°37′W) (1–1–1). Recluse Lake, Man. (56°55′N, 95°45′W) (1–1–1, 1–0–0) (all this survey).

Mackenzie River system. Annette Lake, Jasper National Park, Alta. (1–1–1) (Can. Wildlife Serv.). Baptiste Lake, 12 mi W of Athabasca, Alta. (1–1–1) (this survey). "The Willows", Lake Athabasca (0–0–0) (1945, D. S. Rawson!). Hay River, near mouth [near Hay River, N.W.T.] (0–0–0, 1–1–1) (1917, E. M. Kindle and E. J. Whittaker!; also 1966, R. W. Coleman!). Great Slave Lake, Sulphur Point, N.W.T. (1–1–1) (date? E. J. Whittaker!). Great Slave Lake at Frank Channel (near Rae, N.W.T.) (1–0–1) (1966, R. W. Coleman!). Great Slave Lake (numerous localities) (1–1–1, 1–0–1, 0–0–0) (1946, J. G. Oughton!). Beaver Lake, 30 mi SE of Fort Providence, N.W.T. (1–1–1, 1–0–1, 0–0–0). Birch Lake, Horn River, N.W.T. (1–1–1, 1–1–0) (both 1921, E. J. Whittaker!). Mills Lake, Mackenzie River, N.W.T. (1–1–1, 1–0–1, 0–0–0) (1919, E. M. Kindle and E. J. Whittaker!). Fossil Lake, N.W.T. (66°19′N, 128°55′W) (1–1–1, 0–0–0) (1962, Fish. Res. Bd.!). Lake 30 mi S of Aklavik, N.W.T. (1–1–1) (1940, K. H. Lang!). Aklavik, (1–1–1). (1957, Fish. Res. Bd.!).

Distribution: New Brunswick to Virginia, west in the St. Lawrence and upper Mississippi River drainage areas to Iowa and Nebraska, north in the Canadian Interior Basin to James Bay and Hudson Bay, northwest within tree-line to the mouth of the Mackenzie River, and west to Alberta.

Biology and Ecology: Of 80 *Valvata tricarinata* collections made during this survey, 30 are from large lakes, 4 from small lakes, 2 (only 1 specimen each) from permanent ponds, 6 from back-water areas of large subarctic rivers, 15 from rivers over 100 feet wide, 7 from rivers 50 to 100 feet wide, 8 from rivers 25 to 50 feet wide, 4 from permanent streams 10 to 25 feet wide, and 4 from subarctic muskeg. Bottom sediments were of all types, aquatic vegetation was present at nearly all localities and in lotic habitats current was moderate, slow or not discernible.

Although collecting bias has rather favoured large water bodies, thus affecting the statistical reliability of the results, large numbers of small, permanent ponds, vernal ponds, roadside ditches, or other small and temporary water bodies were also searched. *Valvata tricarinata* was not found in them. In the Canadian Interior Basin, *V. tricarinata* is therefore considered characteristic of perennial water bodies, especially (but not exclusively) of those of considerable size. It is also abundant in subarctic muskeg pools.


Valvata tricarinata Say
45
70°
100°
55°
45°

Baker (1928a: 13-14) has described the soft parts of *Valvata tricarinata*. The body is pinkish-white, with brown blotches on the mantle which show through the shell. The animal moves slowly and evenly. The jaw is covered with rectangular scales. The radula has numerous cusps on the central and lateral teeth which number approximately as follows: 15-1-15 (central), 12-1-16, 12-1-20, and 9-1-25 (laterals).

According to Heard (1963c: 66) egg capsules of *Valvata tricarinata* contain from one to 18 eggs. Hatching occurs in 7 to 15 days.

Remarks: Under " Records " (above) population samples have been coded for presence and absence of carinae on the body whorl following the method proposed by La Rocque (1956: 13). Presence of upper, middle, and lower carinae is indicated by 1-1-1; absence of the lower carina only is indicated by 1-1-0, etc. Angulations do not count as carinations. If more than 1 morph occurs in a single population sample the codes for each morph are given in order of frequency. Notation has been further refined under " Measurements " to indicate the strength of carinae.

By inspection of the carina scores it is evident that the geographical distribution of populations, in which many specimens exhibit loss of 1 carina or more, is largely random. Some populations are much more variable than others in this respect but highly variable populations occur sporadically throughout most of the region. They appear to be absent only from Saskatchewan and Alberta.

Baker's (1928a: 15) generalization that a lake habitat causes reduction of angulation, i.e., that loss of carinae occurs most frequently in lake populations, was not confirmed by the available evidence. Of 46 population samples from lentic habitats, 9 (20%) showed carina reduction. Among the 34 samples from lotic habitats, 6 (18%) showed carina reduction. These results are virtually identical.

The available material was also examined for characters considered significant by other authors, e.g., umbilicus width, direction of slope from upper carina to suture, and relative elevation of spire. Among 23 widely-separated populations studied in detail and analyzed statistically no significance in umbilicus width or in carina-to-suture slope could be seen. Relative elevation of the spire was also quite uniform in general but there were the following exceptions.

Seven collections were made at Klotz Lake, Ontario during 3 different years and all the specimens of *Valvata tricarinata* are similar. They all exhibit an unusually flat spire with the first 2½ whorls planorboid. This causes young specimens to appear much flatter than adults. On the other hand, a large collection from Monument Channel near the portage from Attawapiskat River, 20 mi W of Attawapiskat, Ont., shows that specimens from that popuation are divergent in having unusually tall spires, only the first 1-1½ whorls being planorboid.

In the Canadian Interior Basin, as elsewhere, *Valvata tricarinata* exhibits marked inter-population variation in carination. Many populations also show very substantial intra-population variation in carination. Although reduced carination is rare or absent in western populations, the relationships of morphology and distribution are too poorly defined to justify the recognition of subspecies.

According to Walker (1906: 29, 1918: 130) and Baker (1928a: 18), *Valvata bicarinata* Lea is normally tricarinate

but variable and differs from *V. tricarinata* in being frequently flatter, larger, and having the top of the whorls sloping down from the upper carina to the suture. It is also more southern and eastern in distribution. Baker (loc. cit.) cited no anatomical differences between the 2. The relationship of *V. bicarinata* and *V. tricarinata* cannot be decided from the material at hand but their status as separate species should be reinvestigated.

Superfamily Rissoacea

According to Taylor & Sohl's (1962) summary of gastropod classification, Rissoacea contains 18 families and over 400 genera. The families are similar in that the shells are all small and conispiral, all are operculate, and central teeth of the taenioglossate radulae of many bear small supplementary cusps at their bases. The shells differ markedly in shape and sculpture, however, and the radulae are also quite diverse. Marine, freshwater, and terrestrial genera occur and the superfamily is world-wide. Only the Hydrobiidae are represented in the Canadian Interior Basin.

Family HYDROBIIDAE Troschel

Hydrobiae Troschel, 1857: *Das Gebiss der Schnecken, 1*: 106. Type genus *Hydrobia* Hartmann, 1821.

Shells small, orthostrophic, conispiral or cylindrispiral, holostomatous, umbilicate or non-umbilicate, and smooth or sculptured. Operculum present, corneous or calcareous and paucispiral. Dioecious (in many species sexual dimorphism exists) and phytophagous.

"Animal with a long snout; tentacles long, cylindrical, with the eyes at their outer bases; foot oblong, truncated before, rounded behind; gills internal; verge exserted, placed on the back some distance behind the right tentacle; jaws two; [radula taenioglossate, formula 2-1-1-1-2] central tooth of the radula multicuspid and with one or more basal denticles; laterals hatchet-shaped, multicuspid; marginals slender, multicuspid" (Walker, 1918: 27). Hydrobiidae occur in brackish water and in fresh water.

This is a complex, world-wide group containing many genera (see Wenz, 1938: 555-581). Geologic range: Mesozoic to Recent.

Key to species of Hydrobiidae *

1. Nuclear whorl elevated above second whorl 2
   Nuclear whorl level with second whorl or depressed below it 4
2. Adult shell subglobose (W/L$<$0·70) and very small, i.e., a shell with 4 whorls is not more than $3\frac{1}{2}$ mm high . . . . *Amnicola walkeri* (p 255, Pl. 21, Fig. 9)
   [Adult shell not as above. 3
3. Shell with 4 whorls or more is $3\frac{1}{2}$ to $4\frac{1}{2}$ mm high; umbilicus narrow or absent . . . . . *Marstonia decepta* (p 244, Pl. 21, Fig. 6)
   Shell with 4 whorls or more is more than $4\frac{1}{2}$ mm high; umbilicus wide; shell shaped like a miniature *Campeloma* . . . . . *Cincinnatia cincinnatiensis* (p 241, Pl. 21, Fig. 4)
4. Shell with nuclear whorl coiled in same plane as second whorl; apex blunt; shell conical. *Amnicola limosa* (p 257, Pl. 21, Fig. 10)
   Shell with nuclear whorl sunken below second whorl; apex truncated; shell subcylindrical. *Probythinella lacustris* (p 250, Pl. 21, Fig. 5)

Subfamily Hydrobiinae (*s. str.*)

Verge of males with one functional duct, the vas deferens. This subfamily includes

* The key is based on adult shell characters. Unfortunately these are not always reliable and examination of the radula teeth, length of radula compared with length of shell, and morphology of the male reproductive organs are sometimes necessary for positive identification (see Berry, 1943).

the genera *Cincinnatia*, *Marstonia*, *Probythinella*, *Pyrgulopsis* and other genera, some of which occur in brackish water. See Wenz (1938: 555-571), Morrison (1949: 13-14), and Taylor (1960: 49).

Genus *Cincinnatia* Pilsbry

Cincinnatia Pilsbry, 1891: Land and fresh-water mollusks collected in Yucatan and Mexico. *Proc. Acad. natr. Sci. Philad.*, *43*: 327. Type species: *Amnicola cincinnatiensis* (Anthony) [=*Paludina cincinnatiensis* Anthony] by original designation.

Shell 4-6 mm high; conispiral; relatively thick and solid; nuclear whorl elevated above second whorl and forming an acute apex; whorls rounded and slightly shouldered; umbilicus wide and deep. Radula relatively minute and with small teeth which bear more and smaller cusps than in *Amnicola*. Verge bifid, penis very short and bluntly pointed; secondary lobe much larger than penis; accessory duct absent. (Modified from Berry, 1943: 32).

Only a few species have been assigned to this genus and most of these on shell characters only. Geologic range: Pleistocene to Recent.

Cincinnatia cincinnatiensis (Anthony)
Plate 21, Fig. 4 ; Map 46.

"*Paludina integra* Say," of authors. Original reference: Say, 1821: *J. Acad. natr. Sci. Philad.*, *2*: 174. Say's name is currently applied both to a species of Viviparidae and to a species of Hydrobiidae. The type of *P. integra* is lost but, following Baker (1928a: 67), I believe the name should apply to a species of *Campeloma* (Viviparidae). Sufficient material is not available for proper designation of a neotype population but such a designation should be made.

Paludina cincinnatiensis Anthony, 1840: *Boston J. natr. Hist.*, *3*(1–2): 279, pl. 3: 3. Type locality: "Canal at Cincinnati, Ohio."

Amnicola judayi Baker, 1922: *Nautilus*, *36*(1): 19. Type locality: "Off Doemel Point, Lake Winnebago, [Wisconsin] on a sandy mud bottom in 9 feet of water."

Diagnosis: Shell up to about ¼ inch high, relatively strong, with pointed apex, conical spire, shouldered whorls, and deep umbilicus.

Description: Shell up to 6 mm high, approximately 70% as wide as high, solid, light brown in colour, with roundly ovate aperture which is about half as high as the shell. Whorls up to about 6, convex, shouldered, and separated by deeply incised sutures.

Spire broadly conic with nuclear whorl elevated and forming a roundly pointed apex. Aperture roundly ovate, narrowed above, and with a continuous peristome. Umbilicus wide and deep. Sculpture consisting of fine collabral lines and striae. Operculum thin, paucispiral, and like that of *Amnicola limosa* but without spiral striations.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Traverse Lake, Brown's Valley, Minn.					
Height (H), mm	30	4·5 —5·9	5·07	—	—
W/H	30	0·71—0·80	0·746	0·005	0·027
Ap H/H	30	0·41—0·47	0·440	0·003	0·017
ApW/Ap H	30	0·70—0·83	0·762	0·005	0·027
Whorls	30	5·1 —5·8	5·38	—	—

Feature	N	Range	Mean	S.E.$_M$	S.D.
Red River, 2 mi NE of Drayton, N.D.					
Height (H), mm	12	4·0 —6·0	4·51	—	—
W/H	12	0·65—0·78	0·732	0·010	0·036
ApH/H	12	0·37—0·50	0·447	0·011	0·038
ApW/Ap H	12	0·70—0·81	0·758	0·010	0·035
Whorls	12	5·1 —6·1	5·33	—	—
Bloody Island Camp, Belcher Islands, Hudson Bay.					
Height (H), mm	30	4·0 —5·8	4·79	—	—
W/H	30	0·66—0·82	0·733	0·007	0·041
ApH/H	30	0·38—0·51	0·431	0·006	0·033
ApW/Ap H	30	0·70—0·85	0·762	0·008	0·042
Whorls	30	4·9 —5·7	5·31	—	—

The terms length (L) and height (H) are synonymous when applied to most coiled gastropods. In general, length is used in reference to high-spired groups (e.g., *Lymnaea*) and height in reference to low-spired (e.g., *Valvata*).

The condition of the preserved specimens of all Hydrobiidae used for measurements was such that the animals could not be sexed without breaking or dissolving the shells. According to Baker (1928a: 99, etc.), females of *Amnicola limosa*, *A. walkeri*, *Marstonia decepta* and possibly of *Cincinnatia cincinnatiensis* tend to be relatively shorter and wider than males. The proportion of males to females in the measured samples, unknown in this material, probably affects the range, mean, etc., of the measurements and the ratios, although those quantities may still be considered as representative of unbiased population samples. There appears to be broad overlap in the shell morphology of both sexes, however, since frequency curves of all characters lacked bimodality.

Records:

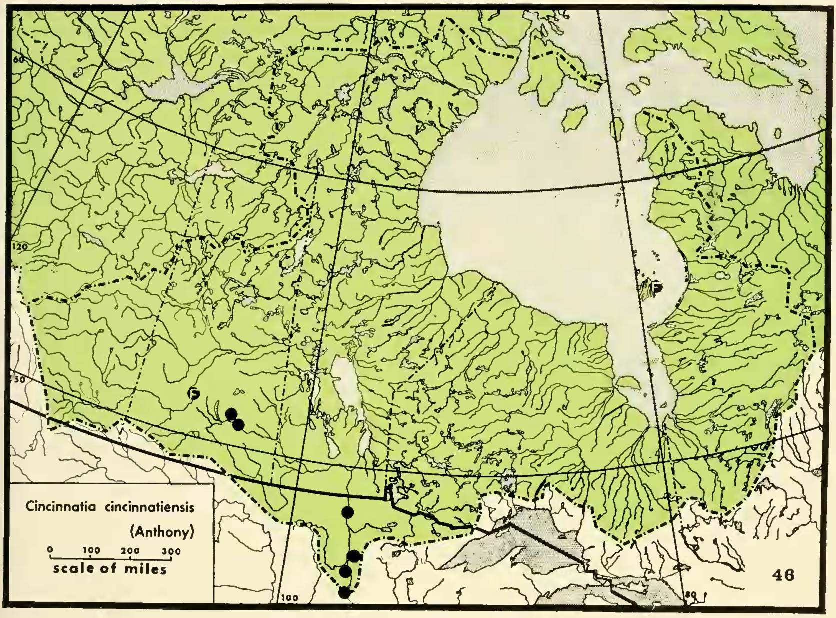
Except for the Echo Lake lot, all records reported here are based on empty, but fresh-looking, shells. They are presumed to represent living populations.

Winnipeg River system. Whitemouth River, Whitemouth, Man. (this survey).

Red River system. Red River drainage: Traverse Lake, south end, Brown's Valley, Minn. Red River, 2 mi NE of Drayton, N.D. Wild Rice River, 9 mi SW of Wahpeton, N.D. Buffalo River, 3 mi E of Stockwood, Minn. (all this survey). Qu'Appelle River drainage: Echo Lake, Sask., dredged in 3·5 to 17 m depth (July 4, 1940, J. S. Thompson!). Qu'Appelle Lake, 4½ mi NW of Katepwa, Sask. (this survey).

Distribution: New York and Pennsylvania west to southern Manitoba, southern Saskatchewan, North Dakota, Utah, and Texas. Empty shells of unknown age also occur on the Belcher Islands in Hudson Bay (see " Remarks ").

Biology and Ecology: Specimens which probably represent living populations were taken at 6 localities during this survey, viz., 2 large lakes, a moderately large river (about 200 feet wide) and 3 smaller rivers (about 60, 50 and 30 feet wide respectively). Submersed vegetation was present in shallow water at all localities and varied from sparse to thick. Bottom deposits were of all types and the current in river habitats was slow to moderate. Berry (1943: 35) found *Cincinnatia cincinnatiensis* alive on soft muddy ooze in Stony Creek, Munroe County, Michigan and on sand



in Lake St. Clair. Vegetation was almost absent at the former locality. As indicated above the Echo Lake specimens were dredged in 3·5 to 17 m depth. Bottom characteristics were not noted.

Berry (op. cit., 33-34) has described the anatomy of this species and has shown it to be strongly divergent from other amnicolids. The foot, the head, the radula, and especially the verge are all morphologically unique. The radula from a specimen 5 mm high was 0·95 mm long. The radula cusp formula is reported to be 20±, 25±, 9-1-4, $\frac{4-1-4}{1-1}$, 4-1-9, 25±, 20± and the teeth are smaller and have more cusps than those of other amnicolids.

Remarks: Although all of the specimens collected during this survey were empty shells many from the vicinity of the Red River had intact periostraca and are presumed to represent living populations. The specimens from Echo Lake, Sask. contained opercula and dried soft parts so the presence of living *Cincinnatia cincinnatiensis* in the upper Qu'Appelle River drainage is certain. The Qu'Appelle Lake lot is therefore also accepted as representing a living population.

Two other sites produced only worn specimens. Those localities are: South Saskatchewan River in a marginal lagoon opposite Cutbank, Sask. (1 shell); and Bloody Island Camp, Belcher Islands, Hudson Bay (100± shells). The South Saskatchewan River locality is close to the Qu'Appelle River and may represent a living population. The Belcher Island locality is particularly interesting because of its isolation. The specimens are almost certainly fossil and may be of hypsithermal age.

The status of *Amnicola judayi* Baker (1922: 19) cannot be decided from available material. Baker (1928a: 125) considered it as the smaller, more rounded, lake form of *Cincinnatia cincinnatiensis* (*s. str.*) but the name *Amnicola integra judayi* has persisted in the literature as a trinomial. Since the geographic ranges of both morphs are concordant and intermediate morphs are known, it is quite certain that a separate taxonomic status for "*judayi*" is not justified.

Genus *Marstonia* Baker

Marstonia Baker, 1926: Nomenclatorial notes on American freshwater Mollusca. *Trans. Wisc. Acad. Arts, Sci. & Letters, 22*: 195. Type species: *Amnicola lustrica* Pilsbry [=*A. lustrica decepta* Baker] by original designation.

Shell up to about 4½ mm high. conispiral, with about 4 to 5 whorls, rather elongated, relatively thin, with the nuclear whorl small and raised above the second whorl, whorls convex and roundly shouldered, umbilicus open but narrow. Radula moderate in length and with the central tooth with 1 basal denticle and a spade-shaped central cusp. "Verge broad at distal end, not bifid, penis at extreme right and projecting from rest of organ. Accessory duct lacking." (Berry, 1943: 29).

Approximately 7 species are recognized as belonging to *Marstonia*. Geologic range: Pleistocene to Recent (Wenz, 1938: 569).

Marstonia decepta (Baker)

Plate 21, Fig. 6; Map 47.

Amnicola lustrica Pilsbry, 1890: Preliminary notes on new Amnicolidae. *Nautilus, 4*(5): 53. Type locality: "New York to Illinois and Minnesota. A species of the Lake drainage." Not *Amnicola lustrica* (Say, 1821) (*nomen oblitum*; =*A. walkeri* Pilsbry, 1898, an objective synonym).

Amnicola lustrica decepta Baker, 1928: *Fresh Water Mollusca of Wisconsin*. Pt. 1, Gastropoda, p 108, text fig. 4. Type locality: "Silver Lake, Waukesha Co., Wis."

Diagnosis: Shell about ⅙ inch high, relatively attenuated, with elevated apex, roundly shouldered whorls, umbilicus narrowly open, and aperture relatively small.

Description: Shell about 4 mm high, about 70% as wide as high (but variable), rather thin, pale to medium brown, with ovate aperture which in most specimens is less than half as high as the shell. Whorls about 4½, convex, roundly shouldered, and separated by deep sutures. Spire conic, with straight or convex sides and a rounded apex. Nuclear whorl raised above second whorl. Aperture ovate, slightly angled above and with a continuous peristome. Umbilicus open but rather narrow. Sculpture consisting of numerous shallow, fine, collabral threads and striae. Operculum thin, paucispiral (about 2½ volutions), oval except pointed at upper edge, and with fine spiral and collabral striae.

See comments on *Marstonia gelida* under "Remarks".

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Klotz Lake, 30 mi E of Longlac, Ont.					
Height (H), mm	22	3·5 —4·2	3·94	—	—
W/H	22	0·71—0·84	0·759	0·007	0·032
ApH/H	22	0·43—0·52	0·474	0·004	0·020
ApW/Ap H	22	0·68—0·88	0·747	0·010	0·046
Whorls	22	4·2 —4·5	4·44	—	—

Feature	N	Range	Mean	$S.E._M$	S.D.
Lake Nipigon, Ont.					
Height (H), mm	6	4·2 —4·5	4·30	—	—
W/H	6	0·71—0·75	0·733	—	—
ApH/H	6	0·48—0·50	0·484	—	—
ApW/Ap H	6	0·73—0·80	0·761	—	—
Whorls	6	4·3 —4·7	4·52	—	—
Wabaskang Lake, 40 mi N of Vermilion Bay, Ont.					
Height (H), mm	3	3·1 —3·8	3·33	—	—
W/H	3	0·68—0·71	0·699	—	—
ApH/H	3	0·39—0·42	0·398	—	—
ApW/Ap H	3	0·75—0·88	0·826	—	—
Whorls	3	4·4 —4·8	4·57	—	—

Records:

Moose River system. Wilson Lake, 1½ mi S of Nellie Lake, Ont. Inlet, east side of Frederick House Lake, 6 mi W of Porquis Junction and ½ mi N of south end of lake, Ont. (both this survey).

Albany River system. Lake Nipigon (1884, J. Macoun!). Klotz Lake, 30 mi E of Longlac, Ont. (this survey).

Winnipeg River system. Botsford Lake, near Drayton, Ont. (1929, A. R. Cahn!). Lac Seul, Ont. (1919, E. W. Waugh!). Wabaskang Lake, 40 mi N of Vermilion Bay, Ont. (this survey).

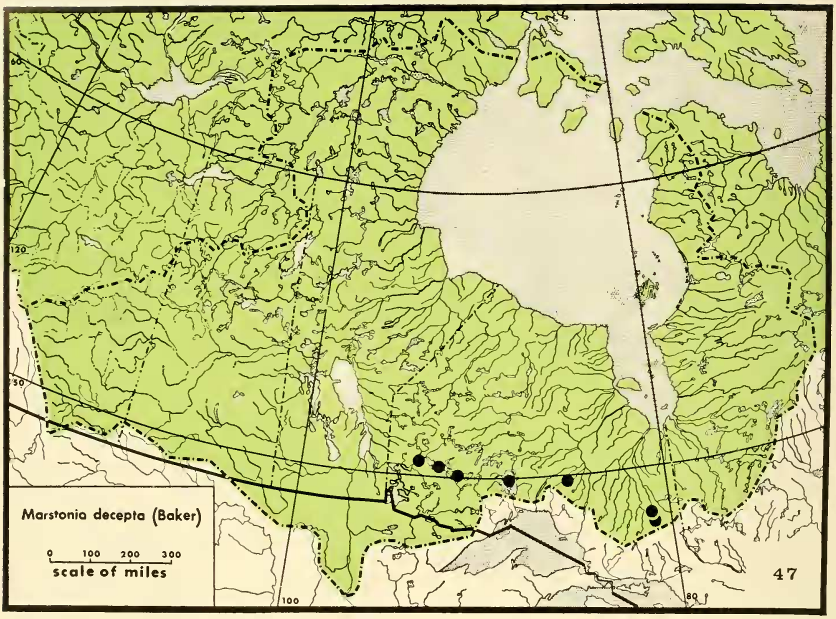
Distribution: Great Lakes and St. Lawrence River system from Minnesota to Pennsylvania, New York, and southern Quebec; adjacent Upper Mississippi River system (southern limit unknown); and some adjacent Hudson Bay drainage areas in Ontario (see " Records ").

Biology and Ecology: Berry (1943: 31-32) has succinctly described the ecology, radula, and reproductive anatomy of this species. Since all specimens taken in the Canadian Interior Basin lacked soft parts (but appeared fresh), most of the following information is taken from his work. Berry writes that: " *Amnicola lustrica* [=*M. decepta*] is often associated with *Amnicola limosa* and inhabits the same type of environment; it occurs on stones in rivers and lakes and on vegetation such as *Vallisneria*, *Potamogeton*, and *Chara*. "

During the present survey *Marstonia decepta* was collected only 4 times, once from the ponded eutrophic part of an inlet into a large mesotrophic lake (very near the lake), twice from large, eutrophic lakes and once from a medium-sized eutrophic lake. Vegetation was moderate to thick at each locality and bottom sediments were of sand, mud and sand or mud.

The verge in *Marstonia decepta* is uniquely shaped and characteristic, being bluntly enlarged distally and with a finger-shaped penis projecting from an outer corner. The radula is relatively small and measured only 0·76 mm in length in a snail 4·3 mm high. The radula cusp formula is 15±, 20+, 4-1-3, $\frac{4-1-4}{1-1}$, 3-1-4, 20+, 15±. The eggs are round and lack the laminate crest seen in the oval eggs of *Amnicola limosa*. Eggs are attached singly to stones or vegetation or are sometimes found floating in clumps at the surface of quiet, shallow pools.

Remarks: Unfortunately the well-known name *Amnicola lustrica* Pilsbry is preoccupied by *A. lustrica* (Say). Another



name for *A. lustrica* Pilsbry must therefore be used. Three names exist which must be considered, *A. lacustris* Pilsbry, *A. lustrica decepta* Baker, and *A. lustrica perlustrica* Baker. Taylor (1960: 51) has selected *decepta* Baker as a substitute for *A. lustrica* Pilsbry. Although Taylor did not discuss the alternatives, *decepta* is probably the only name which is applicable.

J.P.E. Morrison (1947: 86) and H. B. Baker (1964: 174) have both proposed substitution of the name *Amnicola lacustris* Pilsbry, 1891 for *A. lustrica* Pils. (preocc.). But *A. lacustris* is clearly a *lapsus calami*: it appears only in the index to *Nautilus 4* as an error in referring to the description of *A. lustrica* Pils., 1890. Furthermore, recognition of *A. lacustris* Pils. would make *Probythinella lacustris* Baker, 1928a, considered by several recent authors as an *Amnicola* (*s. lat.*), a junior secondary homonym. If *A. lacustris* " Pilsbry " is considered as first validly described by Morrison (1947), it is, in turn, a secondary homonym of "*Amnicola lacustris* Baker " of authors and is untenable, as pointed out by Taylor.

The status of *Amnicola lustrica perlustrica* Baker (1928a: 109), described as larger, wider, and with a smaller umbilicus (etc.) than *A. l. decepta*, is uncertain. It is considered to be characteristic of the Great Lakes and may prove to be a distinct geographic subspecies. One lot from Lake Nipigon (see " Measurements ") is suggestive of *A. l. perlustrica* but more material is needed to evaluate it properly. Specimens from small lakes on islands in the

Great Lakes would be of great assistance in determining whether or not a genetic basis for this morph exists. Such island lakes might be expected to have derived their populations from the surrounding large lake and genetic characters might persist even though the habitat is quite different.

F. C. Baker (1928a: 108) described *Amnicola lustrica decepta* as the ecological variety (i.e., ecophenotype) which occurs in lakes. It is characterized by a wider shell than *A. lustrica* (*s. str.*), and by a wider umbilicus, deeper sutures, and a larger aperture. *A. lustrica* (*s.str.*) was considered to be characteristic of rivers. More recently, Berry (1943: 15, 32; pl. 1: 4-6) has supported the conclusion that such morph-habitat relationships exist and that only one biological species is involved.

The name *Amnicola lustrica decepta* Baker, 1928a, is therefore the only unequivocal and available replacement for *A. lustrica* Pilsbry (*s. str.*). This species is therefore considered here as *Marstonia decepta* (Baker).

Remarks on *Marstonia gelida* (Baker): This Pleistocene species is abundant in beach drift at Denbeigh Point, Lake Winnipegosis, Manitoba (52°52′N, 99°48′W). Single specimens have also been found on two Lake Manitoba beaches (7 mi N of Ashern, Man. and 7 mi N of Moosehorn, Man., all in 1964 by Mr. Marcel Ouellet). These are large range extensions and the first records from Canada. Specimens from Lake Winnepegosis are illustrated on Pl. 21, Figs. 7, 8.

In view of the similarities between *Marstonia gelida* and *M. decepta* and the possibilities of misidentifications, a short discussion of *M. gelida* is appropriate. *M. gelida* was described as *Amnicola lustrica gelida* by F. C. Baker (1921: 22) from "near Morris, Grundy County, Illinois, in marl deposit." It was elevated to species rank (*A. gelida*) and figured by Baker (1928a: 110-111, pl. 6: 19-23, text fig. 45) who reported it from 1 additional specific locality, "Spring Lake east of Green Lake, Green Lake Co., Wisconsin" and 1 general locality "Ohio", both presumably Pleistocene. See also La Rocque, 1968 (p. 390 and figs. 243, 244).

Marstonia gelida may be described briefly as follows: shell about $\frac{1}{6}$ inch high, slender, extremely variable, umbilicate, aperture small and rounded (except angled above), lip thickened, whorls roundly convex and numbering from 5 to 7, sutures deep, and sculpture consisting of well-marked collabral lines or ridges or both. It differs from *M. decepta* in having a more elongate spire, deeper sutures, more rounded whorls and a relatively smaller aperture. It is now (this work) placed in *Marstonia*, but on shell characters only.

A random sub-sample from the Lake Winnipegosis lot was measured for standard characters with the following results.

Feature	N	Range	Mean	$S.E._M$	S.D.
Height (H), mm	30	2·2 —4·0	2·86	—	—
W/H	30	0·49—0·63	0·548	0·007	0·036
ApH/H	30	0·26—0·38	0·318	0·015	0·079
ApW/ApH	30	0·64—0·91	0·800	0·012	0·068
Whorls	30	4·8 —6·7	5·43	—	—

PLATE 21. Viviparidae and Hydrobiidae

FIG. 1. *Campeloma decisum*, Red River at Abercrombie, North Dakota. (NMC 45781, 30 mm) . . . . p 216.

FIG. 2. *Campeloma decisum*, Chukuni River near Red Lake, Ontario (NMC 19331, 31 mm) . . . . p 216.

FIG. 3. *Viviparus intertextus*, " near Rainy Lake, Minn. " (ANSP 12457, 25 mm), ... p 220.

FIG. 4. *Cincinnatia cincinnatiensis*, Traverse Lake, Brown's Valley, Minnesota (NMC 26773, 4·8 mm), ... p 241.

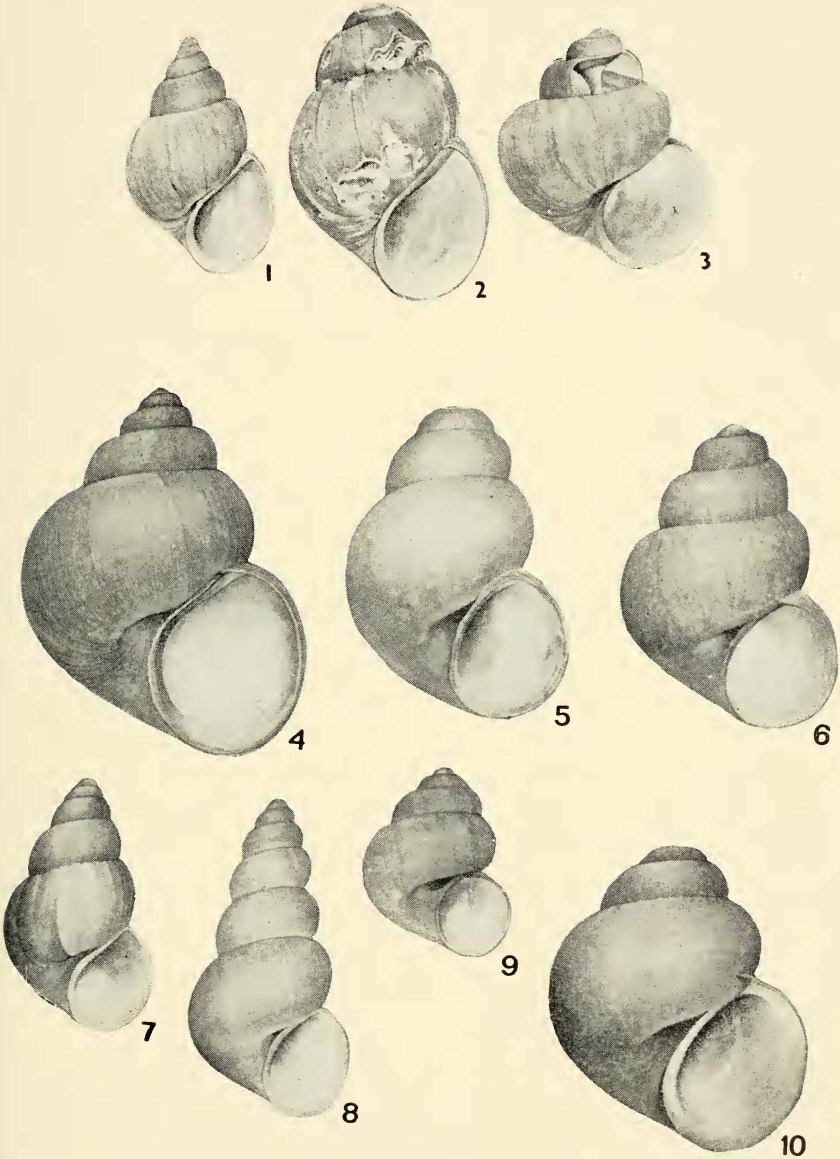
FIG. 5. *Probythinella lacustris*, Black River, Matheson, Ontario (NMC 14968, 3·8 mm), ... p 250.

FIG. 6. *Marstonia decepta*, Wabaskang Lake, 40 mi N of Vermilion Bay, Ontario (NMC 19318, 3·8 mm), ... p 244.

FIGS. 7, 8. *Marstonia gelida*, Denbeigh Point, Lake Winnipegosis, Manitoba (NMC 33096, 3·1 and 4·0 mm) . . , ... , ... p 247,

FIG. 9. *Amnicola walkeri*, Lake Kimmewin, near Drayton, Ontario (NMC 4428, 2·3 mm), ... p 255.

FIG. 10. *Amnicola limosa*, Lac Dubuisson, near Val d'Or, Quebec (NMC 14965, 3·8 mm), ... p 257.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Genus *Probythinella* Thiele

Probythinella Thiele, 1928: Revision des Systems der Hydrobiiden und Melaniiden. *Zool. Jahrb. 55*: 370. Type species: *Paludina emarginata* Kuster [= *Cincinnatia emarginata lacustris* Baker], by original designation.

Vancleaveia Baker, 1930: The molluscan fauna of the southern part of Lake Michigan and its relationship to Old Glacial Lake Chicago. *Trans. Ill. State Acad. Sci., 22*: 191. Type species: *Cincinnatia emarginata canadensis* Baker, by original designation.

Shell about 4 mm high, orthostrophic, subcylindrical, relatively solid, first 1 or 2 nuclear whorls planorboid and sunken below following whorl forming a truncated apex, narrowly umbilicate, aperture holostomatous and ovate, operculum corneous and like *Amnicola* (*s. str.*). Radula minute. Foot very slender and auriculated. Verge bilobed but not bifurcate, right lobe longer than left, accessory duct absent (after Berry, 1943: 36).

In addition to the type species, *Paludina obtusa* Lea is also (provisionally) placed in this genus. Geologic range: Pleistocene to Recent.

Probythinella lacustris (Baker)
Plate 21, Fig. 5; Map 48.

"*Amnicola binneyana* Hannibal" of authors (e.g., Berry, 1943: 36) but not of Hannibal, 1912 (see "Remarks").

Cincinnatia emarginata lacustris Baker, 1928: *Fresh Water Mollusca of Wisconsin*. Pt. 1, Gastropoda, p 127, pl. 7: 20, 21 + text figs. 54: 3, 4. Type locality: "Winnebago Lake, near Oshkosh [Wisconsin]."

Cincinnatia emarginata canadensis Baker, 1928: Op. cit., p 131, text figs. 54: 7, 8. Type locality: "Lake Kakiska, near mouth of Beaver River, west of Great Slave Lake, about latitude 61°." [probably Lake Kakisa near mouth of Kakisa River; locality 5 of Whittaker, 1924: 9].

Probythinella lacustris limafodens Morrison, 1947: *Nautilus, 61*(1): 25–28 (new name for *Paludina emarginata* "Say" Kuster, 1852, invalid). Type locality: "in Nordamerika" (Kuster p 50).

Diagnosis: Shell up to about 1/5 inch high, subcylindrical, rather solid, and with the first 2 whorls immersed and forming a truncated apex.

Description: Shell 3 to 5 mm high, width approximately 70% of height, rather solid, light tan, gray, or white, and with subovate aperture which is about 40% as high as the shell. Whorls about 5, the first 2 planorboid and sunken below he third whorl; the succeeding whorls narrowly expanding and forming a subcylindrical shell. Sutures impressed. Aperture subovate, narrowed adapically, and with a continuous peristome. Umbilicus narrow and deep. Sculpture consisting of growth rests, fine collabral lines and striae, and faint, microscopic spiral striae. Operculum paucispiral, thin, and like that of *Amnicola limosa*.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Fossil Lake, N.W.T. (66°17′N, 128°53′W).					
Height (H), mm	30	3·6 —4·1	3·83	—	—
W/H	30	0·68—0·76	0·720	0·004	0·023
ApH/H	30	0·39—0·45	0·421	0·003	0·016
ApW/ApH	30	0·65—0·81	0·728	0·007	0·040
Whorls	30	4·7 —5·2	4·90	—	—

Feature	N	Range	Mean	S.E.$_M$	S.D.
South Shore of Lake Kakisa near mouth of Kakisa River, N.W.T. (paratypes of *Cincinnatia emarginata canadensis* Baker).					
Height (H), mm	30	2·2 —3·4	2·84	—	—
W/H	30	0·64—0·84	0·727	0·008	0·045
ApH/H	30	0·38—0·47	0·426	0·004	0·023
ApW/ApH	30	0·69—0·92	0·771	0·009	0·049
Whorls	30	4·0 —4·9	4·33	—	—
Black River, Matheson, Ont.					
Height (H), mm	30	3·5 —5·0	4·08	—	—
W/H	30	0·63—0·74	0·672	0·005	0·027
ApH/H	30	0·32—0·46	0·395	0·006	0·032
ApW/ApH	30	0·65—0·82	0·737	0·008	0·046
Whorls	27	4·7 —5·4	4·99	—	—

Records:

Eastern Hudson Bay drainage areas. Bloody Island Camp, Belcher Islands, N.W.T. (subfossil ?) (1959, Fish. Res. Bd.!).

Nottaway River system. Bell River, 23 mi N of Senneterre, Que. (this survey).

Moose River system. Lake Abitibi at Baie la Sarre, 3 mi WNW of Palmarolle, Que.; Black River, Matheson, Ont. (both this survey). Shipsands Island, Moose River estuary, Ont. (1933, H. G. Richards!).

Albany River system. Humboldt Bay, Lake Nipigon, Ont., from whitefish (Berry, 1943: 39). Pagwachuan River, 70 mi W of Hearst, Ont. Klotz Lake, 30 mi E of Longlac, Ont. Stooping River, near junction with Albany River, 12 mi W of Fort Albany, Ont. Inlet of Albany River, 7 mi W of Fort Albany. Muskeg, south side of Albany Island and 2 mi W of eastern end of island, Albany River estuary (all this survey).

Attawapiskat River system. Attawapiskat River, 6 mi W of Attawapiskat, Ont. (this survey).

Winisk River system. Wunnummin Lake, Ont. (52°55′N, 89°10′W) (1962, Ont. Dept. Lands and Forests!).

Severn River system. Magiss Lake (52°59′N, 91°40′W), Nikip Lake (52°53′N, 91°53′W), Sakwaso Lake (53°01′N, 91°55′W) Sachigo Lake, Ont. (1962–64, Ont. Dept. Lands and Forests!). Fort Severn, Ont. (1940, W. B. Scott !).

Winnipeg River system. Pond near Falcon Lake, Man. (this survey).

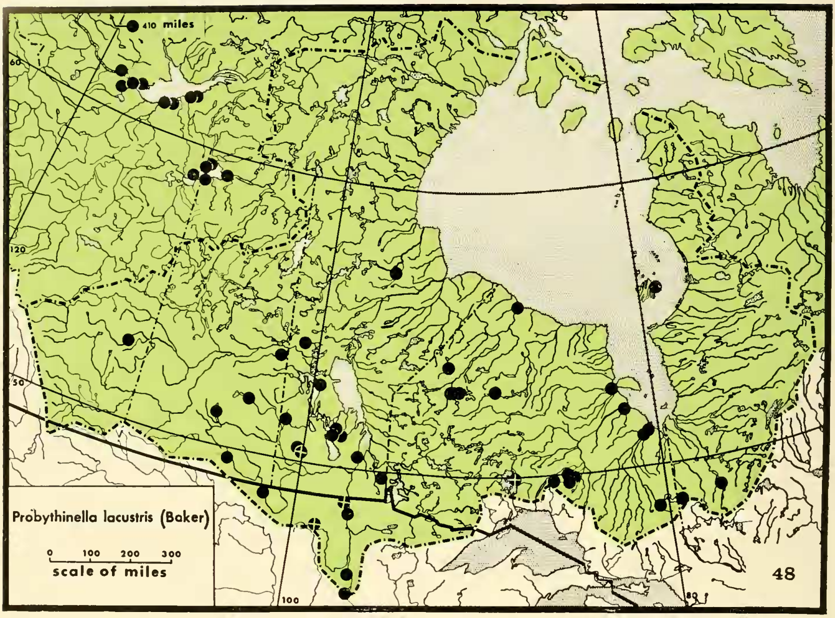
Red River system. Traverse Lake, Brown's Valley, Minn. Red River, 2 mi NE of Drayton, N.D. (both this survey). Red River, Pembina, N.D. Sheyenne River south of Devils Lake (both Hibbard and Taylor, 1960: 81). Wild Rice River, 9 mi SW of Wahpeton, N.D. Tributary of Souris River, 2 mi S of Weyburn city limits, Sask. Souris River [Mouse River], Mouse River Park, 15 mi WNW of Mohall, N.D. Whitesand River, 9 mi ESE of Sheho, Sask. Minnedosa River, 10 mi NNW of Minnedosa, Man. (all this survey). Last Mountain Lake, Sask. (1940, J. S. Thompson!). Shell River, Man. (1887, J. B. Tyrrell!). Clear Lake, Man., from whitefish (Berry, 1943: 39).

Lake Manitoba—Lake Winnipegosis drainage areas. Ebb and Flow Lake, 4 mi NNW of Kinosota, Man. (this survey). Lake Manitoba, east side, 1 mi N of Narrows Ferry; also 15 mi W of Benhorn, Man. Denbeigh Point, northeast corner of Lake Winnipegosis (all subfossil ?; all 1964, M. Ouellet !).

Saskatchewan River system. Carrot River, 24 mi SW of Man.—Sask. boundary and about 50 mi SW of The Pas, Man. (this survey). Cormorant Lake, Man. (1906, W. McInnes!).

Nelson River system. Lake Winnipeg, 20 mi S of Gimli, Man. (this survey).

Churchill River system. Recluse Lake, Little Churchill River, Man. (56°55′N, 95°45′W (this survey).



Mackenzie River system. "The Willows", Lake Athabasca, [Sask. ?], (from whitefish stomachs) (1945, Univ. Sask.!). Great Slave Lake, Sulphur Point, N.W.T. Lake Kakisa, near mouth of Kakisa River (paratypes of *Cincinnatia emarginata canadensis* Baker) (both *ca*. 1921, E. J. Whittaker!). "Little Lake" [Mills Lake], Mackenzie River (1917, E. M. Kindle!). Beaver Lake, 30 mi up Mackenzie River from Fort Providence, N.W.T. (1921, E. J. Whittaker!). Fossil Lake, N.W.T. (66°19′N, 128°55′W) (1962, Fish. Res. Bd.!).

Distribution: According to Baker (1928a: 127), *Probythinella lacustris* ranges in the United States from New York to Iowa south to Kentucky and Arkansas and in Canada to Winnipeg and Hudson Bay. In the Canadian Interior Basin it actually occurs throughout Ontario and Manitoba, in northern Saskatchewan, and in the Northwest Territories south of the tree-line. Empty shells, which may be subfossil, have also been found in drift along the Brazos River at Soaly, Austin Co., Texas by J.C. Bequaert. The subspecies *A. e.* "*canadensis*" (op. cit., p. 130), here considered insufficiently distinct to merit separate taxonomic status, is recorded from Great Slave Lake and the upper Mackenzie River. The records now available indicate that these apparently disjunct ranges are probably continuous.

Biology and Ecology: The 22 localities at which *Probythinella lacustris* was found during this survey are of diverse types, as follows: 6 are large lakes, 1 is a permanent pond, 10 are rivers over 100 feet wide, 3 are rivers from 50 to 100 feet wide and 2 are rivers about 25 feet wide. Current was observed as rapid, moderate, and slow at various river localities but *P. lacustris* was most abundant where the current was slow i.e., in Black River, Matheson,

Ont. (alive) and in Red River, Lockport, Man. (empty shells—river now polluted). Submersed vegetation was present at all localities where living specimens occurred and most frequently it was sparse to moderate. Bottom deposits were of all types with mud or muddy sand predominating. Specimens occurred in all depths from 6 inches (Albany River near James Bay) to 24 feet (Klotz Lake, Ont.)

According to Berry (1943: 36-39) *Probythinella lacustris* is most common in the Great Lakes and in other large lakes. The present data indicate that large lakes are frequently inhabited but that specimens are even more abundant in large rivers and that ponds and small rivers also may harbour the species. This appears to be another example of a species requiring cold water which in the southern part of its range is found only in large, deep lakes.

Berry (loc. cit.) has discussed the anatomy of this species and the following summary is taken from his work. The animal is white and waxy in appearance, the verge is bilobate and characteristic, and the radula is very small, only 0·41 mm long in a specimen 2·9 mm in height. The radula cusp formula is 0, 25±, 12–1–6, $\frac{6\pm\text{-}1\text{-}6\pm}{3\text{-}3}$, 6-1-12, 25±, 0. (The outer marginals have no cusps). *Probythinella lacustris* exhibits positive phototaxis while *Amnicola limosa* does not. The egg capsules have not been observed.

Remarks: The taxonomic history of this species, long known as *Amnicola* (or *Cincinnatia*) *emarginata* Kuster and as *Amnicola binneyana* Hannibal, is quite complex. The former name is based on a misidentification and is invalid (ref. International Commission on Zoological Nomenclature Rules, art. 49). This has all recently been thoroughly discussed by Morrison (1947: 25-28) and by Hibbard & Taylor (1960: 80-84) and need not be repeated here. The latter authors have stated that no consistent relationships are apparent between ecology and shell morphology and that separate subspecific or even separate ecophenotypic designations are not justified. My observations support all these conclusions.

Specimens from Arkansas and Texas were compared with Canadian specimens but no differences greater than those attributable to normal intra-population variation were observed. There does, however, appear to be a tendency for specimens from the Mackenzie River system to have slightly larger umbilici than specimens from elsewhere. It is possible that living material from the Mackenzie River system, when available, will also show soft part differences. If this is so, it may indicate that a population of *Probythinella lacustris* survived and differentiated in the Beringian Refugium. At the present time separate taxonomic status for the Mackenzie River populations appears not to be justified, nowever, and Baker's subspecific name *canadensis* is not used here.

Subfamily Amnicolinae Tryon

Amnicolidae Tryon, 1862: Notes on American fresh water shells, with descriptions of two new species. *Proc. Acad. natr. Sci. Philad.*, p 452.

Verge of males with 2 functional ducts, the vas deferens and "flagellum"; operculum corneous and paucispiral. This subfamily contains the genus *Amnicola* Gould & Haldeman (*in*) Haldeman (1840) and other genera occurring outside of the North American subarctic. See Wenz (1938: 574), Morrison (1949: 13-14, Bithynellinae), and Taylor (1960: 49).

Genus *Amnicola* Gould & Haldeman

Amnicola Gould & Haldeman (*in*) Haldeman, 1840: *A monograph of the freshwater univalve Mollusca of the United States*. Genus *Paludina* Lamarck, p 3 (footnote). Type species: *Paludina lustrica* Say, 1821, by original designation. See " Remarks " below.

Euamnicola Crosse & Fischer, 1891: *Mission Scientifique au Mexique et dans l'Amerique Centrale 2*: 261. (Described as " ou *Amnicola* sensu strictc " and therefore an objective synonym of *Amnicola*.) Type species: *Paludina lustrica* Say, by original explicit implication.

Marstoniopsis Altena, 1936: Remarks on the generic position of *Hydrobia steinii* (*etc*.). *Basteria, 1*: 68. Type species: *Hydrobia steinii* von Martens, by original designation.

Shells between 2 and 5 mm in height; conispiral; with 4 to 5 whorls; nuclear whorl slightly above or level with the second whorl; whorls rounded or slightly shouldered; umbilicus narrow and deep. Radula moderate in size and central tooth with 1 basal denticle. Verge bifid; secondary lobe containing the accessory duct.

Over 30 nominate species have been placed in *Amnicola*. Most occur in North America and a few are Eurasian. Geologic range: Upper Cretaceous (Cenomanian) to Recent (Wenz, 1938: 574).

Remarks: The identity of *Paludina lustrica* Say (1821) has been controversial since its inception. Haldeman first considered it equivalent to *P. limosa* Say [=*Amnicola limosa* (Say)] but later (1845: 16) concluded that it was probably the young of *A. lapidaria* (Say) [=*Pomatiopsis lapidaria* (Say)]. Other authors, including Pilsbry (1890: 53) and F.C. Baker (1928a: 104) identified it with assurance as the young of *P. lapidaria*. Morrison (1947: 84) reviewed the history of the problem and concluded that *P. lustrica* Say was probably congeneric with *A. lustrica* Pilsbry and that the *P. porata* group (and by implication *P. limosa* Say and *A. walkeri* Pils.) should be separated and placed under *Marstoniopsis* Altena, 1936. H. B. Baker (1947: 105) has also commented on the issue and has stated that (1) the "type" of *P. lustrica* in the Philadelphia Academy of Natural Sciences is *Pomatiopsis lapidaria* but that it cannot be the true type specimen and (2) that *Euamnicola* Crosse and Fischer should replace *Amnicola* Gould and Haldeman (*in*) Gould (1841: 228) which is unfortunately preoccupied by *Amnicola* G. & H. (*in*) Haldeman (1840).

More recently Taylor (1960: 49) has discussed the problem again and has argued that *Paludina lustrica* Say is conspecific with *Amnicola walkeri* Pils. (1898). I agree with that opinion.

As long as the identity of *Paludina lustrica* Say is subject to varying interpretations the nomenclatorial stability of *Amnicola* Gould & Haldman (*in*) Haldeman and even of *Pomatiopsis* Tryon are threatened. Both genera are important in the literature of paleontology, ecology, medical malacology, and freshwater malacology in general. It is most desirable that customary usage be maintained. Since all type material of *P. lustrica* Say is lost, the designation of a neotype appears to be the best solution.

A neotype of *Paludina lustrica* Say is hereby designated: it is No. 68798a in the mollusc collection of the Academy of Natural Sciences of Philadelphia. The specimen is also the lectotype (designated by H.B. Baker, 1964: 178) of *Amnicola walkeri* Pilsbry and, of course, is from Lake Michigan at High Island Harbor, Beaver Island, at 10 m depth.

This action will have the following effects: (1) since *Amnicola walkeri* Pilsbry is in the same species group as *Paludina limosa* Say, the name *Amnicola* can be retained in its customary sense (e.g., as in Berry, 1943), (2) since *A. lustrica* Say is a *nomen oblitum*, as pointed out by H.B. Baker (1947: 105; 1964: 174), it does not replace the name

A. walkeri Pilsbry. See also Baker (1960) and Taylor (1961).

Amnicola walkeri Pilsbry
Plate 21, Fig. 9; Map 49.

Paludina lustrica Say, 1821: *J. Acad. natr. Sci. Philad.*, *2*: 175 (Binney reprint, 1858: 69). Type locality: " on the shore of Cayuga Lake." A *nomen oblitum*.

Amnicola Walkeri Pilsbry, 1898: Notes on new and little-known Amnicolidae. *Nautilus*, *12*(4): 43–44. Type locality: " Lake Michigan at High Island Harbor, Beaver Is., at 10 meters depth."

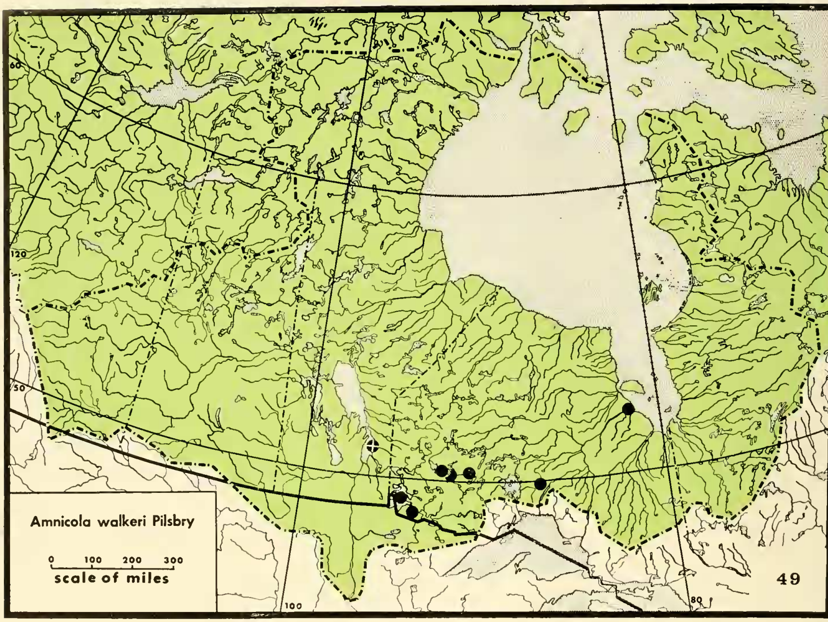
Amnicola walkeri foxensis Baker, 1928: *Fresh Water Mollusca of Wisconsin*, Pt. 1: 116, text figs. 47: 1, 2. Type locality: " Fox River, 1 mile north of Portage, Columbia Co., Wis."

Diagnosis: Shell about 1/10 inch high, with convex whorls, deep sutures, round aperture, conspicuous umbilicus, and short spire.

Description: Shell about $2\frac{1}{2}$ mm high and 70% to 90% as wide as high, thin, light tan in colour (but often covered with a brown deposit) and with a nearly round aperture which is a little less than half the height of the shell. Whorls about 4, convex, increasing rapidly in size, and separated by deep sutures. Apex obtuse, with nuclear whorl rounded and projecting slightly above second whorl. Aperture nearly round but with outer lip more sharply curved than inner lip; peristome continuous and attached to the penultimate whorl for only a short distance. (In *Amnicola limosa* the adnate part of the peristome is distinctly longer). Umbilicus wide and deep. Sculpture consisting of distinct, fine crowded collabral lines. Operculum thin, pale brown, subspiral, and similar to that of *A. limosa*.

Measurements:

Feature	N	Range	Mean
Small Lake 3 mi N of Geraldton, Ont.			
Height (H), mm	5	1·8 —2·6	2·18
W/H	5	0·76—0·87	0·822
ApH/H	5	0·36—0·46	0·414
ApW/ApH	5	0·80—0·92	0·838
Whorls	5	3·4 —4·3	3·86
Pelican Lake, Sioux Lookout, Ont.			
Height (H), mm	5	1·8 —2·5	2·08
W/H	5	0·77—0·96	0·844
ApH/H	5	0·45—0·56	0·490
ApW/ApH	5	0·72—0·83	0·786
Whorls	5	3·4 —4·0	3·74
Outlet of Off Lake, 4 mi NE of Finland, Ont.			
Height (H), mm	5	1·9 —2·3	2·16
W/H	5	0·71—0·76	0·754
ApH/H	5	0·32—0·36	0·339
ApW/ApH	5	0·88—1·00	0·934
Whorls	5	3·2 —4·2	3·88



Records:

Albany River system. Unnamed small lake 3 mi N of Geraldton, Ont. St. Ann's Lake, Sinclair Island, Fort Albany, Ont. (both this survey).

Winnipeg River system. Rainy River Drainage: Outlet of Off Lake, 4 mi NE of Finland, Ont. (this survey). Lake of the Woods, [Ont.] (1884, G. M. Dawson!). English River Drainage: Kimmewin Lake, north of Drayton [Township], Ont. (50°17′N, 91°23′W) (1929, A. R. Cahn!). Pelican Lake, Sioux Lookout, Ont. (this survey). Lac Seul, Ont. (1919, E. W. Waugh!).

Nelson River system. Lake Winnipeg, Victoria Beach, Man. (Mozley, 1938: 117).

Distribution: St. Lawrence River and Great Lakes drainage areas throughout, upper Mississippi River system, the Canadian Interior Basin in the Albany and Winnipeg River systems and in Lake Winnipeg.

Biology and Ecology: Of the 4 localities in which *Amnicola walkeri* was collected during this survey, 1 is a large lake, 2 are small lakes and 1 is a small stream. The stream (outlet of Off Lake) is sluggish, about 25 feet wide and 5 feet deep, and heavily vegetated. Each lake microhabitat was also thickly vegetated and the substrate in all habitats was mud. Baker (1928a: 116) and Berry (1943: 28) similarly report thick vegetation and muddy substrates as the characteristic habitat of *A. walkeri.* Berry also states that a thick accumulation of dead aquatic plants is a requirement but this was not confirmed by the present survey.

Berry (loc. cit.) has described the external soft morphology and reproductive anatomy of this species. The soft parts are heavily pigmented, particularly on and near the head, giving that region

a dark, sooty colour. The verge is strongly bifid. The radula formula is 20±, 20±, 4-1-2, $\frac{4\text{-}1\text{-}4}{1\text{-}1}$, 2-1-4, 20±, 20±. In a specimen whose shell is 2·5 mm high the radula was found to be 0·76 mm long. Each of these characters is an important diagnostic feature for positive identification of *Amnicola walkeri*.

Remarks: For a discussion of the status of *Paludina lustrica* Say see " Remarks " under *Amnicola*.

Amnicola walkeri foxensis was described as an ecophenotype characterized by a smaller umbilicus and occurring in rivers rather than in lakes, the usual habitat of *A. walkeri*. Available data are insufficient to test the reliability of this habitat-morph relationship although some correlations are suggested (see " Measurements ".) There is no evidence that a geographical subspecies is involved, however.

Amnicola limosa (Say)
Plate 21, Fig. 10; Map 50.

Paludina limosa Say, 1817: *J. Acad. natr. Sci. Philad., 1*: 1 (Binney reprint, 1858: 61). Type locality: " muddy shores of the rivers Delaware and Schuylkill, between high and low water marks."

Paludina porata Say, 1821: *J. Acad. natr. Sci. Philad., 2*: 174 (Binney reprint, 1858: 69). Type locality: " Cayuga Lake, [New York]."

Amnicola pallida Haldeman, 1841: *Monograph of the freshwater univalve mollusca of the United States*, Pt. 3, cover, p 3; 1842, Op. cit., Pt. 8: 12, pl. 1: 7. Type locality: " Inhabits Lake Champlain."

Amnicola limosa superiorensis Baker, 1928: *Fresh Water Mollusca of Wisconsin, 1*: 101. Type locality: " Bayfield, Bayfield Co., [Wisconsin], on shore of Lake Superior."

Diagnosis: Shell up to about $\frac{1}{5}$ inch high, conispiral, with a blunt spire, convex, slightly shouldered whorls, ovate aperture, and deep umbilicus.

Description: Shell about 4½ mm high and 3 mm wide, quite thin, yellowish-brown, greyish-brown or tan coloured and with an ovate aperture which is about ½ the height of the shell. Whorls about 4½, convex, slightly shouldered in many specimens, and separated by deep sutures. Spire blunt with the nuclear whorl planorboid; later whorls rounded, slightly shouldered, and increasing slowly in size. Aperture ovate, narrower at the top, and joined to the penultimate whorl by a thin callus. Umbilicus deep and of medium width. Sculpture consisting of narrow, low, crowded collabral lines. Operculum suboval, thin, pale yellowish-brown, with about 2½ volutions, sculptured with spiral and transverse striae and with a dark, spiral line inside of the outer border.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Lac la Ronge, Sask.					
Height (H), mm	30	3·3 —4·2	3·74	—	—
W/H	30	0·69—0·89	0·786	0·008	0·046
ApH/H	30	0·39—0·50	0·439	0·005	0·026
ApW/ApH	30	0·76—1·00	0·899	0·012	0·065
Whorls	30	3·7 —4·4	4·08	—	—

Feature	N	Range	Mean	$S.E._M$	S.D.
Klotz Lake, 30 mi E of Longlac, Ont.					
Height (H), mm	30	3·0 —4·6	3·47	—	—
W/H	30	0·75—0·91	0·825	0·008	0·043
ApH/H	30	0·43—0·50	0·466	0·003	0·019
ApW/ApH	30	0·75—1·00	0·890	0·012	0·066
Whorls	30	2·6 —4·2	3·90	—	—
Duparquet River, 3 mi N of Rapide Danseur, Que.					
Height (H), mm	30	2·8 —4·4	3·49	—	—
W/H	30	0·70—0·85	0·761	0·008	0·042
ApH/H	30	0·39—0·51	0·464	0·005	0·028
ApW/ApH	30	0·68—1·23	0·861	0·017	0·092
Whorls	30	3·5 —4·6	4·11	—	—

Records:

Southern James Bay drainage areas. Eastmain River system: Eastmain River, Eastmain Que. (this survey). Rupert River system: Bordeleau River, 20 mi N of Chibougamau, Que. Rivière à la Perche, 48 mi NE of Chibougamau (both this survey).

Southern and southwestern James Bay drainage areas and southern Hudson Bay drainage areas. Nottaway, Harricanaw, Moose, Albany, Attawapiskat, Winisk, and Severn River systems: Found at all apparently suitable localities where collections were made and presumably abundant throughout the region. Peripheral records are: small creek at Fort Albany, Ont.; Attawapiskat River, ½ mi W of Attawapiskat, Ont.; Shamattawa River, 22 mi S of Winisk, Ont. Unnamed lake, headwaters of Sachigo River, Ont. (53°37′N, 92°40′W) (all this survey).

Hayes River system. Stull Lake, Ont., at outlet (54°29′N, 92°37′W) (this survey).

Winnipeg River system. Numerous records; abundant throughout.

Red River system. Lake Traverse, Brown's Valley, Minn. Red River, Abercrombie., N.D. Lower Red Lake, 1 mi S of outlet, 40 mi WNW of Bemidji, Minn. Rat River, 1½ mi S of La Rochelle, Man. Seine River, 12 mi E of Winnipeg, Man. Outlet of Campbell Lake, 8 mi ENE of Erickson, Man. Whitesand River, 9 mi ESE of Sheho, Sask. Tributary of Souris River, Man. Clear Lake, north shore, 8 mi N of Wasagaming, Man. Minnedosa River, 10 mi NNW of Minnedosa, Man. Minnedosa River, 11 mi NNE of Elphinstone, Man. (all this survey).

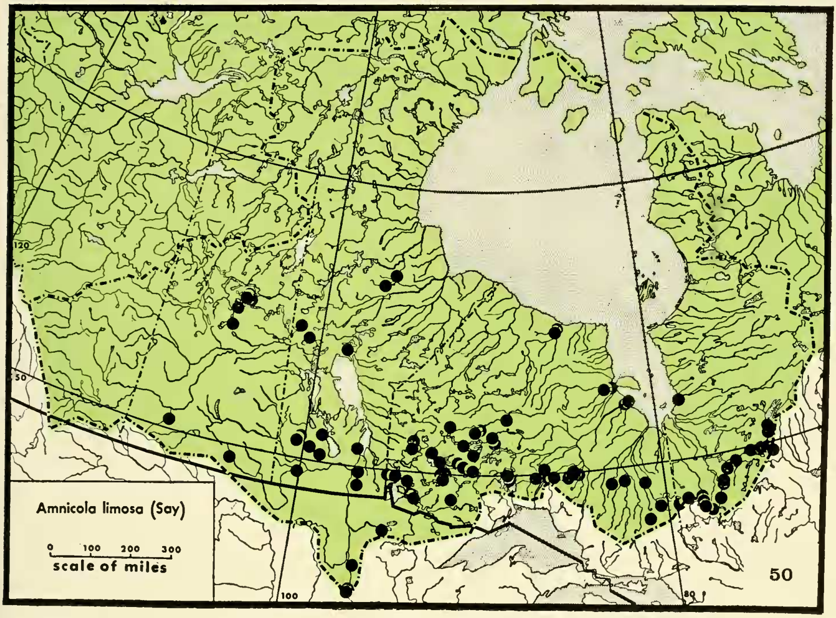
Lake Manitoba drainage area. Whitemud River, Gladstone, Man. Ebb and Flow Lake, 4 mi NNW of Kinosota, Man. (both this survey).

Saskatchewan River system. Swift Current Creek, 3 mi N of Waldeck, Sask. East Channel, Baker's Narrows, Athapapuskow Lake, 22 mi S of Flin Flon, Man. (both this survey). Cormorant Lake, Man. (1906, W. McInnes!).

Nelson River system. Lake Winnipeg, 20 mi S of Gimli, Man. Creek just south of Petersfield, Man. Stout Lake, Ont., at outlet (52°08′N, 94°44′W) (all this survey). Playgreen Lake, Man. (1878, R. Bell!). Limestone Lake, east end, Man. (56°35′N, 96°00′W) (this survey).

Churchill River system. Montreal Lake, south end, 16 mi N of Waskesiu Lake, Sask. Potato Lake, 7 mi S of La Ronge, Sask. Waden Bay, Lac la Ronge (18 foot depth). Lynx Lake, 29 mi N of La Ronge. Recluse Lake, Little Churchill River, Man. (56°55′N, 95°45′W) (all this survey).

Distribution: "New England and New Jersey west to Utah, Manitoba south to Texas" (Baker, 1928a: 97). Also recorded "from Labrador to Florida"



(Berry, 1943: 23). In the Canadian Interior Basin it occurs only south of or slightly beyond the tree-line from the Eastmain River system in Quebec west to the Churchill River system in Saskatchewan and Manitoba. It is much less abundant in the prairies of Manitoba and Saskatchewan than in the boreal forest.

Biology and Ecology: The 96 collections of *Amnicola limosa* obtained during this survey are from the following habitats: 36 are from large lakes, 9 from small lakes, 17 from rivers over 100 feet wide, 8 from rivers 50 to 100 feet wide, 15 from rivers 25 to 50 feet wide, 6 from streams 10 to 25 feet wide and 5 from streams less than 10 feet wide. Current at lotic sites was observed as moderate, slow or imperceptible. Bottom sediments were of all types with mud the more frequent at lotic sites and sand or mud the more frequent at lentic sites. Submersed and emergent vegetation was observed at all localities but 3 and varied from sparse to thick.

In summary, *Amnicola limosa* occurs in all unpolluted, permanent aquatic habitats where macroscopic aquatic vegetation grows. This conclusion is in agreement with other authors (e.g., Baker, 1928a: 97, 99; Berry, 1943: 23; Robertston & Blakeslee, 1948: 84).

The anatomy of *Amnicola limosa* has been described by Baker (1928a: 94-97) and by Berry (1943: 23-25). The living animal is white or pinkish and quite beautiful. A brown streak extends down the side of each tentacle and brown markings occur between the eyes and on the rostrum. The verge is bifurcate and alters its shape when extended (see Berry, 1943 fig. 1). The radula cusp formula is 20±, 15±, 3-1-2.

$\frac{4\text{-}1\text{-}4}{1\text{-}1}$, 2-1-3, 15±, 20±. A specimen 4·3 mm in height had a radula 1·2 mm long. The eggs are laid singly and are usually attached to some solid object. They are ovoid in shape, with pointed ends, and with a laminate crest extending across the dorsal surface from end to end. Egg laying occurs while the water remains warm and extends over a long period each year.

Remarks: As stated by other authors, specimens in some river populations of *Amnicola limosa* tend to be larger than those of lake populations. The name *porata* has been applied to such river populations, often incorrectly in the subspecific sense. The large specimens collected during this survey are almost all from river habitats, but no detailed comparisons have been made.

Berry's (1943: 15) first suggested explanation for this correlation, that rivers become ice-free sooner than lakes and the growing season in rivers is therefore longer, does not appear adequate. Specimens from northern lakes are not significantly smaller than those from southern lakes. His second suggestion, that the current in rivers makes food more available to the snails, appears much more likely although the effect may be an indirect one, involving nutrients for periphyton.

Baker's *Amnicola limosa superiorensis* is described as larger and thicker than *A. l. limosa*. Baker (1939b) also identified specimens from the Rainy River system, Lake of the Woods, and even Prince Albert National Park, Saskatchewan as *A. l. superiorensis* and stated that it was the common amnicolid species from Ontario Lakes. I can see no significant differences between the shells of specimens from Ontario lakes and those farther south. Also since *A. l. superiorensis* was described as an ecophenotype and apparently always considered as an ecologically induced morph by Baker, and there is no evidence that it is more than that, subspecific distinction is unwarranted.

Suborder Pulmonata (Euthyneura, in part).

Pulmonates have no operculum, breathe by means of a pulmonary sac or lung, possess a concentrated nervous system, and are hermaphroditic. Most pulmonates are terrestrial or live in fresh water although a few are marine. The radula contains in each transverse row a central tooth and numerous other teeth which may or may not be clearly separable as laterals or marginals.

The Pulmonata are divided into 3 orders: Basommatophora, Stylommatophora and Systellommatophora based on the number of tentacles and on their characteristics. The Basommatophora possess one pair of retractile tentacles with eyes at the bases of these tentacles. The tentacles may be withdrawn by shortening and thickening. The Basommatophora occur chiefly in freshwater and are well represented in the Canadian Interior Basin. Most Stylommatophora are entirely terrestrial and bear 2 pairs of tentacles with eyes at the tips of the posterior (dorsal) pair. The tentacles can be everted and inverted, but not retracted (except in Succineidae and Athoracophoridae, which are atypical) The Systellommatophora are tropical terrestrial slugs with 2 pairs of tentacles and with eyes on the posterior pair as in Stylommatophora. The tentacles, however, are retractile. See Burch (1968) and Burch & Patterson (1969) for details.

Order Basommatophora

Four superfamilies of Basommatophora occur in the Canadian Interior Basin, viz., Acroloxacea, Lymnacea, Physacea, and Planorbacea. All are hermaphroditic and, although experimental verification

has not been attempted with all species, it is believed that all are facultatively cross- and self-fertilizing. Eggs are deposited in gelatinous masses containing from 1 to many eggs (see Bondesen, 1950).

Superfamily Acroloxacea

As discussed below, Acroloxacea contains only the Family Acroloxidae and represents a primitive group of Basommatophora.

Family ACROLOXIDAE Thiele

Acroloxinae Thiele, 1931: *Handbuch der Systematischen Weichtierkunde*. *2*: 484. Type genus: *Acroloxus* Beck, 1837. Acroloxinae has been placed on the Official List of Family-Group Names in Zoology (Name No. 79) by Declaration 41 of the International Commission on Zoological Nomenclature, 1956. The group was first elevated to family status by Bondesen (1950: 112, etc.).

Shell patelliform, small, and thin; with an ovate aperture; with distinct, crowded, radial microsculpture and widely-spaced concentric growth lines; and with a prominent, acute apex located posterior and to the left of the mid-line. The radula of *Acroloxus lacustris* has 85 to 100 rows of teeth. Each row has 35 to 39 teeth with 1 central and 11 to 14 laterals and 4 to 7 marginals on each side. The central has 4 cusps with the middle 1 largest, the laterals have 7 to 9 cusps and the marginals are without cusps. In *A. coloradensis* the radula is similar but in other species it differs in the arrangement of cusps and in the number of teeth.

The anatomy is superficially similar to that of Ancylidae, except that it is dextral rather than sinistral. Important anatomical differences between the Acroloxidae and Ancylidae, not related to reversed organization, occur in the male and female gonoducts (united in Acroloxidae, mainly separate in Ancylidae and other higher Basommatophora), the radula (a median middle cusp on the central teeth in Acroloxidae, paired main cusps in all Ancylidae, except *Rhodacmea*), the gizzard (absent in Acroloxidae, present in Ancylidae), chromosome number (18 in Acroloxidae, 15, 17, 30 or 60 in Ancylidae) and in histology, cytology, egg capsules and prostate morphology (see Hubendick, 1962 and Burch, 1962 for details).

Hubendick (1962) has shown convincingly that the Acroloxidae and Ancylidae are related only distantly and that the similarities between them are due to covergence both in shell morphology and in the consequential anatomical modifications necessary for successful life as a freshwater limpet. The work of several authors, and especially of Bondesen (1950), Burch (1961, 1962) and Hubendick (1962, 1963), has shown that *Acroloxus* should be considered as a separate, monogeneric family of Basommatophora, more primitive than Lymnaeidae, Physidae, Planorbidae, and Ancylidae, but closer to Lymnaeidae.

Taylor & Sohl (1962: 11, 18) have proposed the further separation of Acroloxidae as Superfamily Acroloxacea, along with recognition of the superfamilies Lymnacea (for Lymnaeidae and Lancidae) and Ancylacea (for Physidae, Planorbidae, and Ancylidae). This separation of Acroloxidae was indirectly supported by Hubendick (1962) who also demonstrated that the Acroloxidae are even more closely related to the distinctive New Zealand Family Latiidae than to the Lymnacea. Acroloxacea is therefore recognized in the present work along with Lymnacea, Physacea and Planorbacea (for Planorbidae and Ancylidae) following .D W. Taylor (ms.).

Genus *Acroloxus* Beck

Acroloxus Beck, 1837: *Index Molluscorum praesentis aevi Musei Principis* . . . Christiani Frederici. Fasciculus primus et secundus Mollusca gastraeopoda pulmonata, p 124. Type

species: *Patella lacustris* L., by subsequent designation (Herrmannsen, 1846: *Index Generum Malacozoorum Primordia*, *1*: 16). *Acroloxus* Beck has been placed on the Official List of Generic Names in Zoology (Name No. 885) by Opinion 263 of the International Commission on Zoological Nomenclature, 1955.

Acroloxus is the only Recent genus within the Family Acroloxidae, which see for shell and anatomical characters. Seven Recent species are known, 6 in Eurasia and 1 (*A. coloradensis*) in North America. The Eurasian species are *A. lacustris* (*L.*), found throughout Europe and northern Asia; *A. improvisus* (Polinski) and *A. macedonicus* (Hadzisce), endemic in Lake Ochrid, Yugoslavia; and *A.* (*Pseudancylastrum*) *kobelti* (Dybowski), *A.* (*P.*) *sibiricum* (Gerstfeldt) and *A.* (*P.*) *troscheli* (Dybowski), endemic in Lake Baikal, U.S.S.R. Acroloxidae are also known from deposits as old as Upper Cretaceous in Europe (subgenus *Pseudancylastrum* Lindholm) and Paleocene in North America (*Palaeancylus* Yen).

Acroloxus coloradensis (Henderson)
Plate 28, Figs. 1-4; Map 51.

Ancylus hendersoni Walker, 1925: *Occ. Papers Mus. Zool., Univ. Mich.*, *165*: 1, pl. 1: 1–2, pl. 2: 1. Type locality: " Eldora Lake, Boulder Co., Colorado" [actually Peterson Lake, 3·4 mi WSW of Nederland, Boulder Co., Colorado, altitude 9245 feet (Bryce, 1970: 105)].

Ancylus coloradensis Henderson, 1939: *Nautilus*, *44*(1): 31. New name for *A. hendersoni* Walker, preoccupied by *A. hendersoni* Walker, 1908, a different specie-.

Diagnosis: Shell limpet-like, up to 1/5 inch long, ovate, and with apex sharply pointed, prominent, directed posteriorly and to the left, and strongly striate.

Description: " Shell oval, slightly wider anteriorly, very much depressed, light horn color; anterior and posterior margins regularly rounded, lateral margins about equally curved, the right somewhat more than the left; anterior, posterior and right lateral slopes straight, left lateral slope slightly incurved; apex very acute, almost spine-like, excentric, turned towards the left side, situated at about 2/5 of the length from the posterior margin and at about 1/3 of the width from the left margin, radially striate, the striae continuing over the surface of the shell from the apex to the margins; surface with fine and regular lines of growth and delicately radially striate. Length 5, width 3, alt. 1 mm. " (Walker, 1925, op. cit.)

Measurements (in mm):

Length*	Width*	Height*	L/W	L/H	W/H	A-PM/L*	A-LM/W*
Pond 6 mi S of Matheson, Ont. (Sta. 177, NMC 22322).							
4·5	3·0	1·0	1·5	4·5	3·0	0·27	0·37
Lac Gabrielle, 10 mi S of Chibougamau, Que. (Sta. 115, NMC 22323).							
4·7	2·7	1·2	1·7	3·9	2·2	0·31	0·28
5·0	2·9	1·1	1·7	4·5	2·6	0·34	0·28

Length*	Width*	Height*	L/W	L/H	W/H	A-PM/L*	A-LM/W*
Lac Caché, 8 mi S of Chibougamau (Sta. 946, NMC 47402).							
3·3	1·8	0·7	1·8	4·7	2·6	0·27	0·39
3·2	1·9	0·7	1·7	4·6	2·7	0·28	0·32
Lac Doré, 4 mi SE of Chibougamau (Sta. 947, NMC 47403).							
4·6	2·9	1·2	1·6	3·8	2·4	0·28	0·38

* A-PM is the distance from the apex to the posterior extremity measured parallel to the midline of the aperture. A-LM is a similar measurement taken from the apex to the left marginal extremity and perpendicular to A-PM.

Records:

Nottaway River system. Lac Doré, 4 mi SE of Chibougamau, Que. (49°52′50″N, 73°10′30″W altitude 1246 feet). Lac Caché, 8 mi S of, Chibougamau (49°49′42″N, 74°25′16″W, altitude 1260 feet). Lac Gabrielle, 10 mi S of Chibougamau (49°47′38″N, 74°25′32″W, altitude 1246 feet) (all Clarke, 1970a and this survey).

Moose River system. Pond 6 mi S of Matheson, Ont. (48°27′30″N, 80°29′10″W, altitude 1125 feet) (Clarke, 1970a and this survey).

Saskatchewan River system. Lost Lake, Glacier National Park, Montana (altitude 4700 feet) (Russell & Brunson, 1967a: 3; 1967b: 33).

Mackenzie River system. Lake Iris (altitude 4285 feet) and lake north of Geikie Station, both in the Miette Valley, Jasper National Park, Alta. (Mozley, 1938: 114).

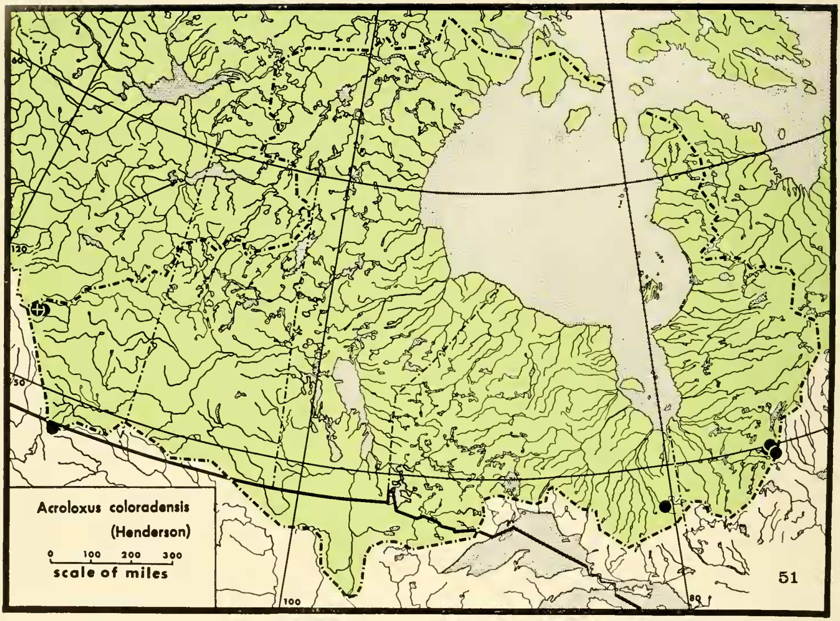
The only additional localities known are (1) a small pond 1½ mi N of Arkell, Nassagawaya Township, Halton Co., Ont. (1967, J. G. Oughton and D. G. S. Wright!, see Clarke, 1970a) and (2) the type locality.

Distribution: A few pond and lake localities in northern Quebec, eastern Ontario, and in the Rocky Mountains in Colorado, Montana and Alberta.

Biology and Ecology: Habitat notes by Henderson (*in* Walker, 1925: 3) regarding the type specimens are as follows: "We found them only clinging to stones, etc., in very tiny inlets from the lake, where they were well protected from the waves, but in clear water, not in swampy ground." Basch (1963a: 413) reports that, according to Henderson's notebooks, "the type specimens were collected on July 28, 1920, in fresh beaver workings at the northwest corner of Eldora Lake, together with '*Pisidium*' *Planorbis*, and four small *Lymnaea*" [See also Bryce (1970)].

The habitat of *Acroloxus coloradensis* in Montana (Lost Lake) is a lake about 2 acres in area and at an altitude of about 4,700 feet (Russell & Brunson, 1967b). The limpets were found on the undersides of rocks near shore in shallow water, vegetation was sparse, and the only other molluscs collected were *Physa gyrina* and *Pisidium casertanum*. The sponge *Spongilla lacustris* was abundant in the lake.

Clarke (1970a) has given more detailed descriptions of the ecology of *A. coloradensis* in Lac Caché and Lac Doré, Que. and the pond near Arkell, Ont.



The lakes are mesotrophic, large, with boulder-cobble substrates in shallow water, and low water hardness (35 ppm Ca CO_3). The limpets occurred in sparse populations (about 1 specimen in 5 square metres of substrate) on cobbles and empty *Anodonta* shells near the shore and in depths of about 12 to 18 inches. Associated organisms include a very few specimens of *Ferrissia parallela*, *Gyraulus deflectus*, *Physa gyrina* and *Amnicola limosa*, the leeches *Nephelopsis obscura* Verrill, *Glossiphonia complanata* L. and *G. stagnalis* L. and the Trichoptera *Helicopsyche borealis* Hagen, *Limnophilus submonilifer* Walker and *Psilotreta indecisa* Walker.

Oughton's field notes (*in* Clarke, 1970a) state that the pond near Arkell, Ontario, occupies a basin of 5 to 10 acres in area but that encroachment by *Typha* has reduced open water to about 75 x 100 feet. The pond bottom is mud and plant detritus and the pond is heavily vegetated. Yellow water lily is dominant and *Riccia*, *Lemna*, *Carex*, and *Nymphaea* were also noted. Other molluscs found during a $\frac{1}{2}$ hour search by two men are *Lymnaea stagnalis* (not common); *Helisoma trivolvis* (few); *Lymnaea elodes* (very few); sparse empty and immature shells of *Physa*, *Planorbula*, and *Gyraulus*; 3 specimens of *Sphaerium* and 1 of *Pisidium*.

H. B. Baker (*in* Walker, 1925: 2) gave a figure of the radula (loc. cit., Pl. 2: 1) and stated its formula as 7-13-1-13-7, finding it very similar to, but smaller than, the European *Ancylus* (now *Acroloxus*) *lacustris*.

In the laboratory *Acroloxus coloradensis* was seen (Clarke, 1970a) to

move slowly, about half as fast as *Ferrissia parallela*. It does not protrude beyond the edge of its shell when in motion. Some of the soft parts are visible through the translucent, horn-coloured shell i.e., a continuous, prominent blackish band along the mantle edge and lying close to the shell margin, the orange to brownish-purple visceral mass (there is color variation between specimens), the dusky head, and the 2 black eyes. Viewed from below the dark mantle band is seen to bear approximately 100 small, bright blue, elongate processes (apparently papillae) lying across the mantle band and directed toward the mantle edge. The foot and head are of moderate width, flecked with grey on a pale purplish-brown background, and not unlike the foot and head of a *Ferrissia parallela* from Lac Doré. In general the body appears similar to that of *Acroloxus lacustris* as figured by Hubendick (1962, fig. 3).

The 3 living specimens observed deposited 6 egg capsules. The capsules were lenticular-ovate, from 1·9 to 3·4 mm long, with double, transparent walls, pale yellow lumen, and with either 2 or 3 eggs in each capsule. The eggs measured from 0·5 x 0·8 to about 0·6 x 1·2 mm, were ovate in shape, and colorless or faintly whitish. The egg capsules and eggs resemble those of *Acroloxus lacustris* figured by Bondesen (1950: 64) in general shape and in that the eggs are loosely packed. They appear to differ in the possession of yellow lumen (not mentioned for *A. lacustris*) and in the smaller number of eggs in each capsule. Surface striae of the capsules, as mentioned for *A. lacustris* by Bondesen, were not observed through the walls of the culture dishes.

Remarks: The Recent distribution of *Acroloxus coloradensis* in North America, i.e., with populations in the Rocky Mountains from Colorado to Alberta and in north-central Quebec (and in eastern Ontario), may be indicative of a much wider geographical range in previous time. The early Pleistocene records in Kansas and Nebraska (Taylor, 1960: 61) support this. The similarities between *A. coloradensis* and *A. lacustris* imply that the 2 species are closely related. There is no direct evidence available to indicate whether *Acroloxus* used the Pleistocene Beringian land bridge or not.

It is quite possible that *Acroloxus coloradensis* is even now more widely distributed in North America than the Recent records indicate. As reported by Henderson (*in* Basch, 1963a: 413), by Russell & Brunson (1967b : 33), and in some detail by Clarke (1970a) it occupies a seemingly inhospitable habitat and one which is not searched thoroughly by most collectors. In the Quebec localities in June, adults which had overwintered also occurred in low densities. It appears probable that this primitive species may be adapted to survive in specialized habitats where predator pressures are low and competition from more advanced limpets and other molluscs is less intense.

Superfamily Lymnacea

According to the classification here adopted, this superfamily contains only the Family Lymnaeidae. Characteristics of that family are described below.

Family LYMNAEIDAE Rafinesque

Lymnaeidae (correction of "Lymnidia") Rafinesque, 1815: *Analyse de la Nature*: 144 (Binney & Tryon reprint, 1864: 18). Type genus: *Lymnaea* Lamarck, 1799. Placed on the Official List of Family-Group Names in Zoology by decision of the International Commission on Zoological Nomenclature (Opinion 495).

Shells small to large, thin or of moderate thickness, orthostrophic and conispiral (and elongate in most species) or patelliform (*Lanx*), and non-operculate. Conispiral species are holostomatous, with aperture typically angled above and rounded below, umbilicate or non-umbilicate, and sculptured with collabral lines and with or without periostracal ridges, surface malleations, and additional microsculpture. Monoecious (with facultative cross- and self-fertilization) and phytophagous.

" Animal dextral. Head with a broad short muzzle dilated at the end. Foot rounded behind. Tentacles flattened. Jaw composed of three plates, a large one in the centre, and two small, narrow laterals. Radula broad; central tooth small, simple or bicuspid, the laterals bi- or tricuspid. The marginals bi-, tri- or multicuspid or serriform. " (Walker, 1918: 5).

This is a world-wide family but it is most abundant in the Holarctic. Its geological range extends from the Jurassic to the Recent. Hubendick (1951) recognizes 2 subfamilies of Lymnaeidae, i.e., Lymnaeinae, and Lancinae, the former containing only the genus *Lymnaea* and the latter only the limpet-like genus *Lanx*.

Walter (1969) considers that *Lanx* and *Lymnaea catascopium* are anatomically so similar that separation of *Lanx* and *Lymnaea*, even at the generic or subgeneric level, is unwarranted. *Lanx* does not occur in the Canadian Interior Basin, but it appears to be monophyletic and I consider that on conchological and genetic grounds it deserves at least generic rank. Geologic range of Lymnaeidae: Upper Jurassic to Recent (Zilch, 1959: 91). The total number of Recent species is probably of the order of 100.

The most comprehensive works on Lymnaeidae in this century are by Baker (1911, which see for prior works), Baker (1928a) and Hubendick (1951). Their classifications, which are divergent, are considered substantially incorrect by Walter (1968 and pers. comm.) on the basis of extensive and detailed anatomical studies. The most complete anatomical study of a lymnaeid (*Lymnaea catascopium*) is also by Walter (1969).

Subgroups within the conispiral Lymnaeidae have been in general use in North America for more than 50 years. Studies by Walter indicate that these subdivisions are, in large part, artificial, that some species combine characters of more than 1 group, and that between subdivisions lack of concordance of anatomical and shell characters is frequently encountered. Both Hubendick and Walter have recommended that formal subgroup divisions in *Lymnaea* be abandoned.

Walter (1968 and pers. comm.) has brought to light convincing evidence indicating that the main line of lymnaeid evolution has progressed through 5 stages. These stages are defined chiefly on reproductive anatomical features and have been designated as radicine, prostagnicoline, and primitive, intermediate, and advanced stagnicoline. Five living species possess anatomical features which correspond with these stages. They are *Lymnaea ollula* Gould (eastern Asia), *L. luteola* Lamarck (India), *L. corvus* Gmelin (Europe), *L.* species (England), and *L. catascopium* Say (North America). Walter further believes that all other species complexes within *Lymnaea* are related to these categories and may represent successive adaptive radiations from the main evolutionary line.

" In the rise of the " higher " Lymnaeidae, the primary anatomical changes evidently were: reduction of the ancestrally long and simple penis to an almost vestigial state, and its re-evolution, with acquisition of a penial knot, and radial and other special musculature, as part of a copulatory holdfast mechanism; narrow-

ing of the vagina proper, and its acquisition of a powerful sphincter, as part of that mechanism; loss and re-evolution of the uterine caecum; enlargement, then reduction, of the prostatic tract, its change from a unifolded to a multifolded condition then reversion to the former condition, its sharp division into 2 " prostates, " and finally, rapid development of a prostate pouch. Concurrent trends affected muscularity, glandularity, conformity, and size of the reproductive organs as a whole. Evidently, reversions are important in lymnaeid evolution, producing chimaeras which look like intergeneric hybrids, and giving the impression that the phylogenetic pattern is reticulate. " (Walter, 1968: 19).

This evolutionary sequence and the informal groupings proposed by Walter have been adopted in the present work. In addition I have introduced vernacular names such as fossariaform, bulimneaform, etc. where appropriate to designate species complexes.

KEY TO THE SPECIES AND SUBSPECIES OF LYMNAEIDAE

1. Shell large, 35 mm high or higher 2
   Shell medium-sized or small, less than 35 mm high 6
2. Shell with open umbilicus and, in many populations, heavily sculptured 3
   Shell without open umbilicus and not heavily sculptured, except rarely in individual specimens 4
3. Spire low, sutures well-marked but not deep, whorls not inflated. Range: northern Saskatchewan and northern Manitoba . . . . *Lymnaea catascopium preblei* (p 349, Pl. 23, Fig. 3)
   Spire medium to high, sutures deep, whorls inflated. Range: northern British Columbia to Alaska and northwestern Northwest Territories . . . . *Lymnaea atkaensis* (p 308, Pl. 23, Fig. 2)
4. Shell relatively thin but strong, spire rather short and (in many specimens) with slightly convex sides, aperture brownish or purplish within . . . . *Lymnaea megasoma* (p 293, Pl. 12, Figs. 2, 3)
   Shell thin and brittle, spire medium to long and with concave sides, aperture not brownish or purplish 5
5. Aperture length more than 60% of shell length, spire relatively short and of about 4 whorls. Upper Great Lakes and adjacent Canadian Interior Basin only . . . . *Lymnaea stagnalis sanctaemariae* (p 305, Pl. 23, Fig. 1)
   Aperture length less than 60% of shell length, spire relatively long and of about 5 to 6 whorls. Common and widely distributed . . . . *Lymnaea stagnalis appressa* (p 296, Pl. 12, Fig. 1)
6. Shell small to medium-sized with medium-sized aperture and with numerous spiral, microscopic, blade-like periostracal ridges *Lymnaea caperata* (p 313, Pl. 22, Fig. 10)
   Shell not as above 7
7. Shell small to medium-sized, thin, similar to *Succinea* in appearance, with about 4 whorls, short spire, capacious body whorl and large, ovate aperture. Range: southern Manitoba (rare), St. Lawrence River drainage area, and south . . . . *Lymnaea columella* (p 290, Pl. 22, Fig. 12)
   Shell not as above 8
8. Shell less than 10 mm high 9
   Shell more than 10 mm high 17
9. Shell with more than 4 whorls 10
   Shell with less than 4 whorls (juvenile specimens of most stagnicolaform *Lymnaea*) 17
10. Shell solid, inflated, with heavy columella callus and relatively large aperture (Ap L/L approximately 0·62 to 0·81). Range: Great Lakes, Rainy Lake, and Lake-of-the-Woods region . . . . *Lymnaea catascopium nasoni* (p 347, Pl. 23, Fig. 4)
    Not as above 11
11. Shell moderately broad, with convex whorls, shiny periostracum, and with microsculpture consisting, at least in part, of spiral rows of tiny crescents. Known range: foothills and mountains of Alberta (rare) and western United States . . . . . *Lymnaea montanensis* (p 317, Pl. 22, Fig. 11)
    Not as above 12
12. Shell highly variable, body whorl dominant and columella area expanded. Lateral teeth of radula bicuspid. Range: southern Saskatchewan to southern British Columbia and western United States . . . . . *Lymnaea bulimoides* (p 283, Pl. 22, Figs. 5-8)
    Not as above 13
13. Whorls rounded. Lateral teeth of radula tricuspid 14

Whorls weakly to strongly shouldered. Lateral teeth of radula tricuspid or bicuspid 15

14. Relative length moderate (morph *modicella*) or elongate (morph *rustica*), with whorls flatly rounded, sutures well-marked but not deep, umbilicus small but open, and aperture ovate . . . . *Lymnaea modicella* (p 276, Pl. 22, Fig. 3)
Relative length moderate, with whorls well-rounded, sutures deep, umbilicus partly obscured by reflexed lip, and aperture rounded . . . . *Lymnaea parva* (p 279, Pl. 22, Fig. 4)

15. Spire longer than aperture and with high, roundly shouldered whorls, which are about as high as wide or higher than wide . . . . *Lymnaea exigua* (p 273, Pl. 22, Fig. 2)
Spire about as long as aperture; spire whorls wider than high 16

16. Shell very small (less than 6 mm high), thin, with convex, shouldered whorls and with outer lip broadly rounded. Lateral teeth of radula bicuspid . . . . *Lymnaea dalli* (p 288, Pl. 22, Fig. 9)
Shell small, but often more than 6 mm high, of moderate thickness, with strongly shouldered whorls and with outer lip laterally flattened. Lateral teeth of radula tricuspid . . . . *Lymnaea decampi* (p 269, Pl. 22, Fig. 1)

17. Shell up to about 15 mm high when the animal is fully grown (i.e., with 6 to 6½ whorls), with convex whorls and shiny periostracum. Known range: foothills and mountains of Alberta (rare) and far-western United States . . . . *Lymnaea montanensis* (p 317, Pl. 22, Fig. 11)
Shell not as above 18

18. Shell relatively broad (W/L>0·55) 19
Shell relatively narrow (W/L<0·55) 22

19. Adult specimens (i.e., with 6 whorls or more) not exceeding 22 mm in height; columella wide and thick. Range: subarctic and arctic Canada and Alaska . . . . *Lymnaea arctica* (p 319, Pl. 12, Figs. 4–6)
Adult specimens exceeding 22 mm 20

20. Spire high or moderate and acute, whorls inflated and strongly shouldered, sutures deep. Range: northern British Columbia to Alaska and northwestern Northwest Territories . . . . *Lymnaea atkaensis* (p 308, Pl. 23, Fig. 2)
Spire low or moderate, whorls flattened to convex but not inflated. Widespread but not occurring in Alaska or in northwestern Canada 21

21. Shell inflated, relatively thin, heavily sculptured (in most specimens) and strongly shouldered. Range: northern Saskatchewan and northern Manitoba . . . . *Lymnaea catascopium preblei* (p 349, Pl. 23, Fig. 3)
Shell variable but in most populations it is relatively heavy but not heavily sculptured or strongly shouldered. Widely distributed in southern Canada and northern United States . . . . *Lymnaea catascopium* (*s. str.*) (p 328, Pl. 12, Figs. 7, 8)

22. Aperture relatively small (Ap L/L<0·45), columella heavy, shell length not exceeding 22 mm. Range: vicinity of Coronation Gulf and Dolphin and Union Strait (Arctic Ocean) in northwestern Northwest Territories . . . . *Lymnaea kennicotti* (p 323, Pl. 23, Fig. 5)
Not as above 23

23. Shell narrow and relatively elongate (W/L<0·40), whorls flat-sided. Some specimens exhibit alternating, zebra-like, light and dark collabral bands. Widely distributed in southern Canada and northern United States . . . . *Lymnaea reflexa* (p 358, Pl. 23, Figs. 7, 8)
Shell relatively wider (W/L>0·40) and not as above 24

24. Shell with large rotund body whorl and sharply acute spire, which appears pinched in many specimens. Range: Alberta, British Columbia and far-Western United States . . . . *Lymnaea proxima* (p 355, Pl. 23, Fig. 6)
Shell not as above 25

25. Adult specimens (i.e., with 6 or more whorls) variable but not exceeding 22 mm in height; columella wide and thick. Range: subarctic and arctic Canada and Alaska *Lymnaea arctica* (p 319, Pl. 12, Figs. 4–6)
Adult specimens variable, often exceeding 22 mm in height; columella strong but not wide and thick. Widespread and abundant in southern Canada and northern United States . . . . *Lymnaea elodes* (p 351, Pl. 12, Figs. 9, 10)

Genus *Lymnaea* Lamarck

Lymnaea Lamarck, 1799: Prodrome d'une nouvelle classification des coquilles (*etc.*). *Mém. Soc. Hist. natr. Paris*, *1*: 75. Type species *Helix stagnalis* L. by subsequent designation (Fleming, 1818). Placed on the Official List

of Generic Names in Zoology by decision of the International Commission on Zoological Nomenclature (Opinion 495).

Galba of autnors, but doubtfully cf F. Schrank, 1803: *Fauna Boica, 3*(2): 262, 285. Type species *Galba pusilla* Schrank, by monctypy (*G. pusilla* is unidentifiable).

Stagnicola Leach (*in*) Jeffreys, of authors. Original reference is: Jeffreys, 1833: *Trans. Linnean Soc. London, 16*: 376. Type species *Stagnicola communis* Leach (ms.) (first published in synonymy under *Buccinum palustris* Müller, by Jeffreys (loc. cit.) and therefore an objective synonym of that name) by monotypy. See " Remarks " under *L. elodes* (Say).

Bulimnea Haldeman, 1841: *A monograph of the freshwater univalve mollusca of the United States*. Pt. 3 (Genus *Limnaea*, Lamarck): 6. Type species *Lymnaeus megasomus* Say, by original designation.

Fossaria Westerlund, 1885: *Fauna in der paläarktischen Region lebenden Binnenconchylien. 5*: 49. Type species "*Lymnus truncatula* Muller" [=*Buccinum truncatulum* O. F. Muller] by subsequent designation (Pilsbry & Bequaert, 1927: 107).

Pseudosuccinea Baker, 1908: *Science, 27*: 943. Type species: *Lymnaea columella* Say, by original designation.

Pseudogalba F. C. Baker, 1913: *Nautilus, 26*: 120. New name for *Simpsonia* Baker, 1911 (p 236), not Rochebrune, 1905 (molluscs). Type species *Lymnaea humilis* Say, by original designation.

Hinkleyia Baker, 1928: *Fresh Water Mollusca of Wisconsin*. Pt. 1, Gastropoda, p 259. Type species *Lymnaeus caperatus* Say, by original designation.

Nasonia Baker, 1928: *Fresh Water Mollusca of Wisconsin*, Pt. 1, Gastropoda, p 195, 264. Type species *Limnaea cubensis*, by original designation.

Bakerilymnaea Weyrauch, 1964: Nomenklatorische Bemerkungen. *Arch. Mollusken., 93*(3/4): 169. New name for *Nasonia* Baker, 1928 *non* Ashmead, 1864 (Hymenoptera).

Shell and soft parts with characters of the Family Lymnaeidae (exclusive of *Lanx*).

Prostagnicoline Fossariaform Species

Formerly *Fossaria* Westerlund, 1885 (=" *Galba* Schrank, 1803 " of numerous authors and *Pseudogalba* F. C. Baker, 1913 of Baker). See synonymy under *Lymnaea*.

Shells, small, variable, with a pointed spire, small (0·4-0·5 mm) nuclear whorls and smooth columella. Radula with tricuspid lateral teeth. Fossariaform species have been recorded from the Pliocene (Taylor, 1960: 32) to the Recent.

Lymnaea decampi (Streng)

Plate 22, Fig. 1; Map 52.

Limnaea desidiosa var. *De Campi* Streng 1896: A new variety of *Limnaea*. *Nautilus, 9*(11): 123, text figs. Type locality: " Brook's Lake, Newaygo Co., Mich."

Diagnosis: Shell small to very small, rather solid, with whorls strongly shouldered, outer lip laterally flattened, and aperture adapically narrowed and arched.

Description: Shell small (usual maximum length about $\frac{1}{3}$ inch), of moderate thickness, variable, with aperture and spire about the same length, and with shouldered whorls and laterally flattened aperture. Nuclear whorls satiny, forming a bluntly rounded apex, and brown in colour. The brown colour extends in many specimens to the penultimate whorl and contrasts with the whitish body whorl. Whorls about 5, convex, roundly to abruptly shouldered (the body whorl is strongly shouldered) separated by deeply impressed sutures, and forming a short, acute spire. Aperture of medium size, narrow, abruptly rounded and arched above and broadly rounded below. Outer and inner lips thin, the outer lip flattened laterally and the inner lip narrowly reflected and, in its lower part, erect. Umbilical chink prominent and bordered by the inner lip. Sculpture consisting of numerous fine, closely spaced collabral lines and ridges and a few irregularly spaced growth rests.

Measurements:

Feature	N	Range	Mean	S.E.$_{M}$	S.D.
Klotz Lake, 30 mi E of Longlac, Ont.					
Length (L), mm	20	3·3 — 5·5	4·40	—	—
Width (W), mm	20	1·8 — 2·8	2·16	—	—
W/L	20	0·43 — 0·54	0·493	0·006	0·025
Ap L/L	20	0·47 — 0·63	0·554	0·009	0·038
Whorls	19	3·8 — 5·2	4·41	—	—
Clear Lake, 8 mi N of Wasagaming, Man.					
Length (L), mm	18	3·6 — 7·2	5·36	—	—
Width (W), mm	18	2·1 — 4·1	2·93	—	—
W/L	18	0·52 — 0·57	0·550	0·004	0·017
Ap L/L	18	0·49 — 0·57	0·519	0·004	0·019
Whorls	15	4·0 — 5·0	4·61	—	—
Halkett Lake, 20 mi S of Waskesiu Lake, Sask.					
Length (L), mm	30	7·9 —11·5	9·14	—	—
Width (W), mm	30	3·9 — 5·6	4·77	—	—
W/L	30	0·47 — 0·59	0·522	0·005	0·025
Ap L/L	30	0·45 — 0·57	0·506	0·005	0·030
Whorls	27	5·2 — 6·0	5·41	—	—

Records:

Albany River system, Ont. Kabinakagami River, (50°11′N, 84°15′W) (1967, B. C. McDonald!). Klotz Lake, 30 mi E of Longlac. Kenogamisis Lake, 7 mi SE of Geraldton. Hutchinson Lake, 5 mi N of Geraldton. Small pond connected to Orient Bay, Lake Nipigon, 20 mi S of Beardmore. Lake 1 mi W of Jellicoe. (all this survey). Bamaji and Cat lakes and outlet of Kapikik Lake. (Baker & Cahn, 1931: 54).

Attawapiskat River system, Ont. "Ojiski" [=Ozhiski] Lake. Kawinogans River [=Crow River] (both 1904, W. McInnes!). Blind channel of Monument Channel at portage, 20 mi W of Attawapiskat. Attawapiskat River, 8 mi W and 6 mi W of Attawapiskat (all this survey).

Winisk River system, Ont. Side channel of Winisk River, 15 mi S of Winisk. (this survey).

Severn River system, Ont. Severn Lake, north end (54°05′N, 90°42′W) (this survey).

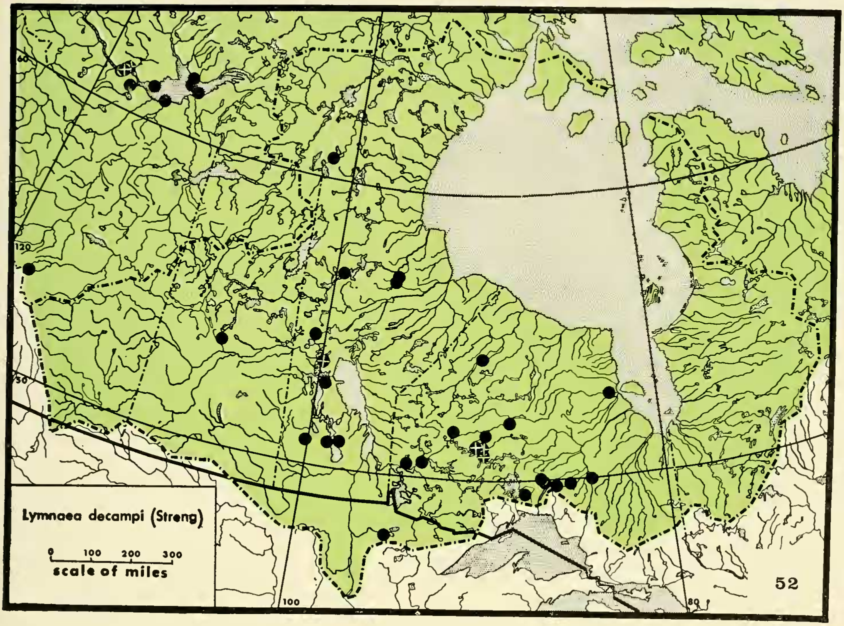
Winnipeg River system. Hamilton and Pashkokogan lakes, Ont. (Baker & Cahn, 1931: 54). Vermilion Lake, Vermilion Bay, Ont. Wabaskang Lake, 40 mi N of Vermilion Bay. (both this survey).

Red River system. Lower Red Lake, 1 mi S of outlet and about 40 mi NNW of Bemidji, Minn. Clear Lake, north shore and south shore, near Wasagaming, Man. (both this survey).

Saskatchewan River system. Halkett Lake, 20 mi S of Waskesiu Lake, Sask. (this survey).

Lake Manitoba—Lake Winnipegosis drainage areas. Ebb and Flow Lake, 4 mi NNW of Kinosota, Man. (this survey). Lake Manitoba, east side, 1 mi N of The Narrows, Man. Denbeigh Point, Lake Winnipegosis, Man. (both 1964, M. Ouellet!).

Nelson River system. Atikameg Lake, Man. (Mozley, 1938: 99). Unnamed lake 27 mi E of



Simonhouse, Man. Limestone Lake, east end, Man. (56°35′N, 96°00′W) (both this survey).

Churchill River system. Lac la Ronge, Sask. (from whitefish) (1954, Univ. Sask.!). Opachuanau Lake, Man. (56°44′N, 99°37′W). Recluse Lake, Man. (56°55′N, 95°45′W) (both this survey).

Kazan River system. Southwest end of Ennadai Lake, N.W.T. (60°45′N, 101°46′W) (this survey).

Mackenzie River system. Edith Lake, Jasper National Park, Alta. (1964, R. W. Coleman!). Athabasca River near Waterways, Alta. Great Slave Lake N.W.T., several localities (all 1944–46, J. G. Oughton!). Kakisa Lake, N.W.T. (*ca*. 1940, W. Kennedy!). "Little Lake" [Mills Lake] at mouth of Horn River N.W.T. (Whittaker, 1924: 11). Beaver Lake, Mackenzie River 30 mi above Fort Providence, N.W.T. (1921, E. J. Whittaker!).

Distribution: Great Lakes-St. Lawrence River basin northward in the region west of James Bay to the Attawapiskat and Severn River systems, and northwestward in the boreal forest region to the vicinity of Great Slave Lake. As pointed out by Baker (1911: 290) and La Rocque (1963:33, 34, etc.) *Lymnaea decampi* is abundant in Wisconsin (Pleistocene) deposits in the Illinois-Ohio-New York region.

Biology and Ecology: *Lymnaea decampi* was found at 21 localities during this survey. Fourteen of these are large lakes, 3 are small lakes, 1 is a permanent pond, and 3 are rivers over 50 feet in width. The river localities, 2 in the Attawapiskat River and 1 in the Winisk River, are all in northern Ontario near the northern climatic limit of the species. Vegetation was thick or of medium abundance in habitats where the species was taken alive. Fresh empty shells which were abundant on the exposed shore of several large lakes (e.g., Clear Lake and Limestone Lake, Man. Halkett Lake, Sask., and Ennadai

Lake, N.W.T.) were not found in shallow water nearby and presumably occur alive in deeper water offshore. *L. decampi* was dredged alive in Klotz Lake, Ont. on June 2, 1965, at a depth of 5 feet and far from shore among submersed *Potamogeton* which had just begun annual growth and had not yet reached the surface.

Mozley (1938: 100) has given the habitat of this species as " lakes of moderate or large size, usually those which have clear and cold waters. " This is amply supported by present data, although the clear, cold water of slow flowing northern rivers also provides a suitable habitat. The evidence indicates that *Lymnaea decampi* needs cold, highly oxygenated water for survival. See " Remarks " below.

Nothing has been published regarding the anatomy or radula of *Lymnaea decampi*. Specimens collected from 2 localities during the present survey were examined for radula characteristics, with the following results: Monument Channel at portage to Attawapiskat River, 20 mi W of Attawapiskat, Ont., 3 specimens, formulae 23-1-22 (shell length 7·1 mm), 21-1-20 (6·8 mm), and 21-1-19 (6·7 mm); outlet of Severn Lake, Ont., 2 specimens, formulae 20-1-19 (5·9 mm) and 23-1-22 (4·9 mm). Each specimen had 6 tricuspid lateral teeth on either side of the central and marginal teeth with 4 to 5 cusps.

A number of very small juveniles of *Lymnaea decampi* were collected on August 25, 1961 in Vermilion Lake, Vermilion Bay, Ontario. This probably indicates that egg laying and juvenile emergence occur in mid- or late summer when water temperatures in large lakes approach their maxima.

Species frequently found associated with *Lymnaea decampi* are *L. stagnalis appressa*, *Anodonta grandis simpsoniana*, and several species of *Helisoma*.

Remarks: Baker (1911) and all subsequent authors prior to 1967 (except Hubendick, 1951) have considered *Lymnaea decampi* to be a subspecies of *L. obrussa* Say. Differences in morphology, ecology, zoogeography, and geological history show that they are distinct species, however (Clarke, 1968). Gibson (1967: 15) has also suggested, tentatively and independently, that this is the case.

Lymnaea decampi is similar to *L. obrussa* but is readily separable from it. *L. decampi* is more strongly shouldered than *L. obrussa*, the aperture is more narrowed adapically, the body whorl near the outer lip is more flattened laterally, and the maximum length of *L. decampi* (about 12 mm) is much less than that of *L. obrussa* (about 19 mm).

The ecology of the 2 species is quite different. *L. decampi* occurs in cold-water lakes and rivers whereas *L. obrussa* is " found generally in small bodies of water, as creeks, ponds, sloughs, bays, and marshy spots along river banks " (Baker, 1911: 281).

Zoogeographically, *Lymnaea decampi* occurs only in the Great Lakes - St. Lawrence River region and northwest in the subarctic boreal forest region. *L. obrussa* extends from the Great Lakes - St. Lawrence River region south to the Gulf of Mexico and west to California. It is not found in the subarctic.

Finally, Pleistocene deposits show that the geographical ranges of both *Lymnaea obrussa* and *L. decampi* were, as expected, much more southern during the Wisconsin Stage than they are at present. Both species later extended their distribution northward and during the hypsithermal period they may well have extended farther north than they do today. Such translocations must have provided sufficient opportunity

for hybridization so that if genetically based reproductive isolation had not been operative the species would have hybridized and would not now exist as separate entities.

Hubendick (1951 : 127-128) has synonymized all North American species and subspecies of fossariaform *Lymnaea* together with *L. caperata*, under *L. humilis* Say. Specimens of *L. caperata* were not seen by him, but the decision to synonymize all nominate species of fossariaform lymnaeids must also have been based on inadequate material. Detailed examination of sufficient numbers of specimens proves unquestionably that several distinct species of fossariaform *Lymnaea* occur in boreal North America and that *L. caperata*, with its sharp periostracal ridges, is one of the most distinctive species we have.

Lymnaea exigua (Lea)
Plate 22, Fig. 2; Map 53.

Lymnea exigua Lea, 1841: *Proc. Amer. phil. Soc.*, *2*: 33. Type locality: "Tennessee."
Lymnea planulata Lea, 1841: *Proc. Amer. phil. Soc.*, *2*: 33. Type locality: "White Sulphur Springs, Virginia."
Lymnea plica Lea, 1841: *Proc. Amer. phil. Soc.*, *2*: 33. Type locality: "Tennessee."

Diagnosis: Shell small, narrow, attenuated with high, roundly shouldered whorls which are approximately as high as wide or higher than wide.

Description: Shell small (up to nearly ½ inch long), rather thin, subfusiform, relatively narrow, and with an elongate spire which, in most specimens, is taller than the aperture. Colour light brown throughout or, in some northern populations, with whitish body whorl and penultimate whorl and with brown earlier whorls (see "Remarks"). Nuclear whorls satiny and dome-shaped. Whorls about 5½, flatly rounded and roundly shouldered. Spire whorls as high as wide or higher than wide. Sutures deeply impressed. Body whorl flattened, subcylindrical, and about ⅔ the length of the whole shell. Aperture ovate and slightly effuse at the base. Outer lip thin, slightly reflected, and with the lower part nearly erect. Umbilicus small and narrowly open or closed by the reflected inner lip. Sculpture consisting of fine collabral lines, irregular growth rests, and (in some specimens) poorly defined spiral lines.

Measurements:

Feature	N	Range	Mean	S.E. $_M$	S.D.
Fort Frances, Ont.					
Length (L), mm	5	5·1 —8·0	6·52	—	—
Width (W), mm	5	2·4 —3·8	3·10	—	—
W/L	5	0·47 —0·48	0·475	—	—
Ap L/L	5	0·43 —0·49	0·467	—	—
Ap W/Ap L	5	0·52 —0·57	0·544	—	—
Whorls	5	4·7 —5·1	4·88	—	—

Feature	N	Range	Mean	S.E.$_M$	S.D.
Monument Channel, 6 mi W of Attawapiskat, Ont.					
Length (L), mm	25	4·4 —7·0	5·84	—	—
Width (W), mm	25	2·2 —3·5	2·86	—	—
W/L	25	0·44 —0·53	0·491	0·005	0·025
Ap L/L	25	0·48 —0·58	0·515	0·005	0·025
Ap W/Ap L	25	0·42 —0·56	0·515	0·006	0·032
Whorls	25	4·4 —5·1	4·79	—	—
Shamattawa River, 22 mi S of Winisk, Ont.					
Length (L), mm	25	4·1 —7·7	6·24	—	—
Width (W), mm	25	2·1 —3·7	2·98	—	—
W/L	25	0·43 —0·56	0·486	0·007	0·036
Ap L/L	25	0·46 —0·57	0·513	0·005	0·027
Ap W/Ap L	25	0·44 —0·56	0·486	0·005	0·024
Whorls	25	4·5 —5·4	4·92	—	—

Records:

Moose River system. Inlet of Frederickhouse Lake, 6 mi W of Porquis Junction, Ont. Moose River, 8–10 mi S of Moosonee, Ont. (both this survey).

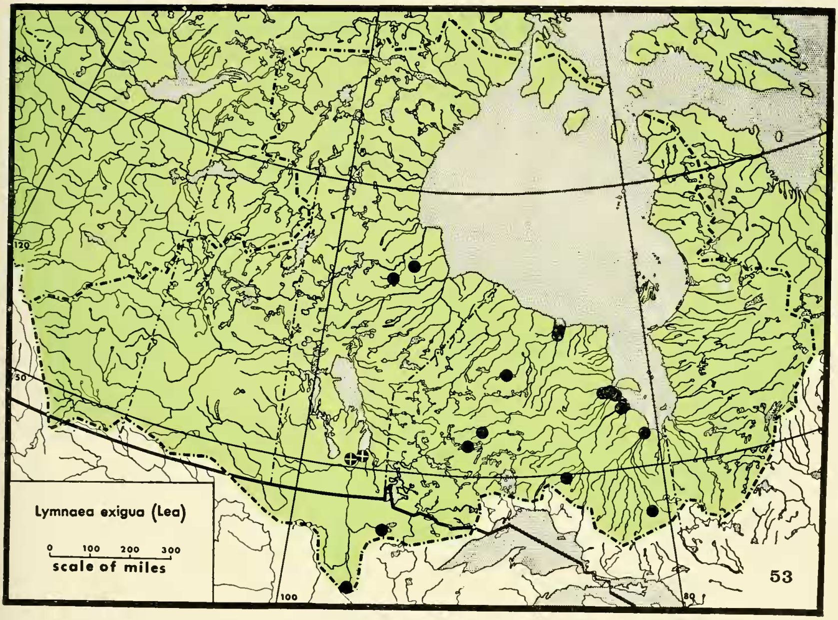
Albany River system. Lake Nipigon, Ont. (1884, J. Macoun!). Klotz Lake, 30 mi E of Longlac, Ont. Mouth of Stooping River, 12 mi W of Fort Albany, Ont. Side channels of Albany River, 9 mi W of Fort Albany. Ox-bow pond at Devil's Gut, near Albany Island, Albany River estuary. (all this survey).

Attawapiskat River system. Small stream 4 mi W of Pickle Crow, Ont. Side channel of Attawapiskat River, 17 mi W and 6 mi W of Attawapiskat, Ont. (two localities). Monument Channel, 12 mi W and 6 mi W of Attawapiskat (two localities). Muskeg near small creek 1 mi E of Attawapiskat (all this survey).

Winisk River system. Shibogama Lake, west end, Ont. (53°31′N, 88°35′W). Cove on west side of Shamattawa River, 1 mi S of junction with Winisk River and 22 mi S of Winisk, Ont. Short channel off Shamattawa River, ½ mi S of junction with Winisk River. Cove on west side of Winisk River, ½ mi E of mouth of Shamattawa River. Mouth of small tributary of Winisk River 16 mi S of Winisk. Narrow side channel of Winisk River 15 mi S of Winisk. Small ponds in marsh 6 mi E of Winisk (all this survey).

Winnipeg River system. Outlet of Bamaji Lake, Ont. (1929, A. R. Cahn!). Pond near Fort Frances, Ont. (date ?, F. R. Latchford!). Onion Lake, near Minaki, Ont. (Mozley, 1938: 100). "Railway ditch near Birch River, Man. Mile 69, G.W.W.D. Ry." [=near Reynolds, Man.] (Mozley, 1926a: 125, 1938: 100).

Red River system. Traverse Lake, Brown's



Valley, Minn. Lower Red Lake, 1 mi S of outlet and 40 mi NNW of Bemidji, Minn. (both this survey). Clandyboye, Man. (Mozley, 1938: 100).

Nelson River system. " Creek running into the Grand Marais, at a point 2 mi east of Balsam Bay, [Lake Winnipeg] Man." (Mozley, 1938: 100).

Owl River system. Owl Lake, Man. (56°22′N, 94°35′W) (this survey).

Churchill River system. Recluse Lake, Man. (56°55′N, 95°45′W) (this survey).

Distribution: Maine and throughout the St. Lawrence River system, south to Alabama in the Mississippi-Missouri River basin, north to the Hudson Bay Lowlands in northern Ontario, and west to the Red River and Lake Winnipeg region in Minnesota and Manitoba, Not recorded from deposits older than Recent.

Biology and Ecology: Twenty-two lots of *Lymnaea exigua* were collected during this survey. Two are from large eutrophic lakes, 4 are from eutrophic bays in large mesotrophic lakes, 2 are from small mesotrophic lakes, 2 are from subarctic muskeg and 12 are from slow-moving or backwater parts of large, medium-sized, and small rivers (down to 10 feet in width). Vegetation was present at all localities and was thick or moderately abundant at most. Bottom sediments were of all types from rocks and gravel to mud and clay.

Mozley (1938: 100) gives the habitat of *Lymnaea exigua* as " usually in small marshy streams, or on the protected shores of small lakes. " We may now add protected parts of large lakes, backwater areas of rivers, and subarctic muskeg to the list of acceptable habitats.

The anatomy and radula of this species have been described by Baker

(1911: 286; 1928a: 302) as similar in general to *Lymnaea obrussa*. The marginal radular teeth were found to begin on the 7th tooth in *L. exigua* while in *L. obrussa* they begin on the 11th, however. The 1st lateral teeth are reported as tricuspid and the gross formula given is 25-1-25.

Specimens of *Lymnaea exigua* collected during this survey from the Winisk River near the Shamattawa River in northern Ontario gave radula formulae of 21-1-20 (shell length 8·8 mm), 21-1-20 (8·8 mm) and 21-1-21 (7·6 mm). The marginal teeth of these specimens begin with the 11th tooth, the 10th tooth being transitional. See " Remarks " below.

Remarks: Although *Lymnaea exigua* is uncommon throughout most of its range, it is conspicuously abundant in the Winisk and Attawapiskat River systems of Northern Ontario. In the Winisk River system it occurred in every permanent-water habitat visited. In the Attawapiskat River system it occurred in about half of these habitats. The specimens from that region are much paler in colour than those from farther south, the body whorl and penultimate whorls of the northern specimens (and the foot and head regions) being whitish whereas in more southern specimens the shells are uniformly brownish. Examination of the radula of Winisk River specimens also showed apparent differences from the radular characteristics reported in the literature, although the 25-1-25 count reported by Baker may have been from a larger specimen than any examined here. Shell measurements of population samples from the north, when compared with those from Rockland, Maine (USNM 336651), showed no significant differences, however, and other lots from elsewhere in the United States also appear similar in relative dimensions. Although there is evidence (colour and apparent radular differences) that the Winisk and Attawapiskat River populations may constitute a distinct subspecies it is considered prudent to defer such a decision until much more preserved material is available for comparison.

Lymnaea modicella (Say)
Plate 22, Fig. 3; Map 54.

Lymneus modicellus Say, 1825: *J. Acad. natr. Sci. Philad.*, *5*: 122 (Binney reprint 1858: 113). Type locality: " Oswego, on the Susquehanna River, near the State of New York " [Owego, New York].

Lymnea rustica Lea, 1841: *Proc. Amer. phil. Soc.*, *2*: 33. Type locality: " Poland, Ohio."

Diagnosis: Shell small, moderately or markedly elongate, with flatly rounded whorls, sutures well marked but not deep, small umbilicus, and ovate aperture.

Description: Shell small (maximum length less than ½ inch), light brown or yellowish-brown, relatively thin, with the spire about the same length as the aperture or slightly longer with flatly rounded whorls and ovate aperture. Nuclear whorls satiny, bluntly dome-shaped, and grayish-brown. Whorls 5 to 5½, moderately convex and rounded, and forming a medium-long or relatively elongate, acute spire. Aperture sub-elliptical and slightly elongate. Outer lip thin and convex. Inner lip slightly thickened, narrow, turned up or somewhat reflected, fairly straight or bent just above the umbilicus, and in some specimens partly obscuring the umbilicus. Umbilicus small and open or partly closed. Sculpture consisting of numerous fine collabral lines and ridges, a few irregularly spaced growth rests, and in some specimens also of numerous fine spiral lines.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Recluse Lake, Man. (56°35′N, 95°45′W).					
Length (L), mm	2	7·1, 9·4	8·25	—	—
Width (W), mm	2	3·6, 5·0	4·30	—	—
W/L	2	0·51, 0·53	0·520	—	—
Ap L/L	2	0·52, 0·54	0·532	—	—
Ap W/Ap L	2	0·46, 0·47	0·465	—	—
Whorls	2	5·0, 5·2	5·10	—	—
Attawapiskat River, ½ mi W of Attawapiskat, Ont.					
Length (L), mm	6	3·4 —6·0	5·10	—	—
Width (W), mm	6	1·8 —3·1	2·68	—	—
W/L	6	0·51—0·55	0·526	—	—
Ap L/L	6	0·47—0·56	0·512	—	—
Ap W/Ap L	6	0·52—0·58	0·532	—	—
Whorls	6	4·0 —4·8	4·48	—	—
Moose River, 8–10 mi S of Moosonee, Ont.					
Length (L), mm	20	5·4 —8·3	7·23	—	—
Width (W), mm	20	2·9 —3·8	3·47	—	—
W/L	20	0·44—0·54	0·483	0·007	0·030
Ap L/L	20	0·44—0·50	0·467	0·004	0·020
Ap W/Ap L	20	0·49—0·59	0·548	0·006	0·025
Whorls	20	4·8 —5·4	5·08	—	—

Records:

Abbreviations: *m*=*modicella* morph, *r*=*rustica* morph. See " Remarks ".

Eastmain River system. Eastmain River in backwater and along shore, both near Eastmain, Que. (*m*) (this survey).

Nottaway River system. Bell River, Senneterre Que. (*m*) (this survey).

Moose River system. Moose River, 8–10 mi S of Moosonee, Ont. (*m*+*r*). Frederickhouse River, 6 mi N of Cochrane, Ont. (*m*) (both this survey).

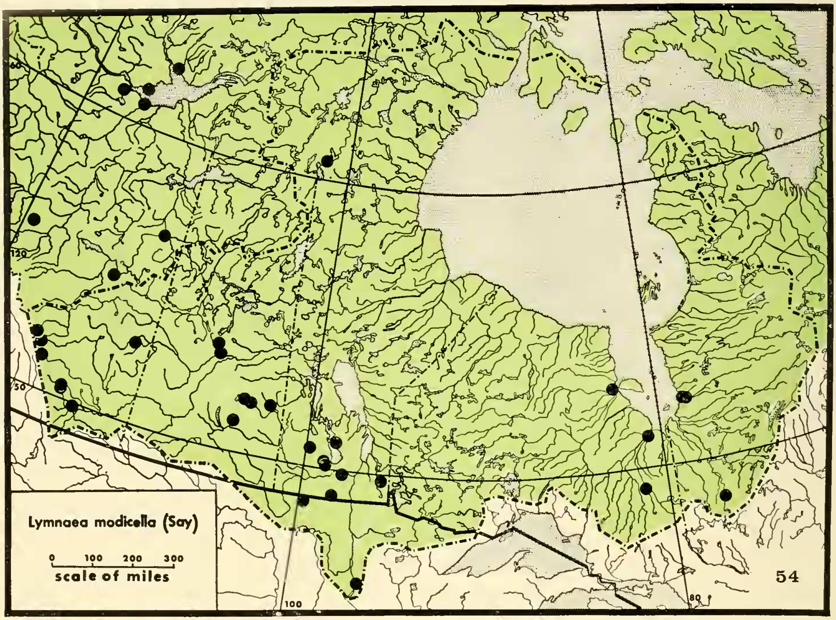
Attawapiskat River system. Narrow channel off Attawapiskat River, ½ mi W of Attawapiskat, Ont. (*m*) (this survey).

Winnipeg River system. Roadside ditch 10 mi W of Falcon Lake, Man. (*r*) (this survey).

Red River system. Lake Traverse, Brown's Valley, Minn. (*r*). Lake Traverse outlet, 7 mi NW of Wheaton, Minn. at Minn.—S. Dak. boundary (*m*). Pembina River, 6 mi N of Windygates, Man. (*m*). La Salle River, Elie, Man. (*m*). Qu'Appelle Lake, 4½ mi NW of Katepwa, Sask. (*m*+*r*). Whitesand River, 9 mi ESE of Sheho, Sask. (*m*+*r*). Assiniboine River, 2 mi W of Preeceville, Sask. (*r*). Shell River, 9 mi NNE of Roblin, Man. (*r*). Creek outlet of Campbell Lake, 8 mi ENE of Erickson, Man. (*r*) (all this survey).

Devil's Lake drainage area, (inland drainage). Grand Lake, 6 mi NW of St. John, N.D. (*r*) (this survey).

Lake Manitoba—Lake Winnipegosis drainage area. Whitemud River. Gladstone, Man. (*m*) (this survey). Lake Manitoba, east side,



1 mi N of Narrows ferry (*m*) (1964, M. Ouellet!).

Quill Lakes drainage area, (inland drainage). Little Quill Lake, Sask. (*r*) (1920, collector?).

Saskatchewan River system. South Saskatchewan River drainage area: Cayley, Alta. (*r*+*m*). 6 mi S of High River, Alta. (*m*) (both 1966, R. Hartland-Rowe!). Small pool near Oldman River, 1 mi W of Monarch, Alta. (*r*). Second Vermilion Lake, Banff, Alta. (*r*). Hector Lake, 10 mi NNW of Lake Louise, Alta. (*r*) (all this survey). North Saskatchewan River drainage area: "Wainwright Park", Wainwright, Alta (*m*) (1932, W. E. Swales!). Shell River, 6 mi W of Prince Albert, Sask. (*r*). Halkett Lake 20 mi S of Waskesiu Lake, Sask. (*r*) (both this survey).

Churchill River system. Recluse Lake, Little Churchill River, Man. (56°55′N, 95°45′W) (*r*) (this survey).

Kazan River system. Ennadai Lake, 1 mi N of entrance of Kazan River, N.W.T. (60°45′N, 101°46′W), (*r*) (this survey).

Mackenzie River system. Peace River drainage area. 6 mi SE of Hythe, Alta. (*m*) (1963, F. R. Cook!). Athabasca River drainage area. Shore of Athabasca River at mouth of Tawatinaw River, Athabasca, Alta. (*r*) (this survey). Mouth of Hay River, N.W.T. (*m*) (1921, E. J. Whittaker!). Great Slave Lake, several localities (1944-46, J. G. Oughton!).

Distribution: Most of the United States (except the South Atlantic States) and in Canada from the Great Lakes-St. Lawrence River system west and northwest to the Churchill, upper Mackenzie, and Yukon River systems. Not recorded from deposits older than Recent.

Biology and Ecology: Of the 25 collections of *Lymnaea modicella* made during this survey, 3 are from large lakes, 4 from small lakes, 1 from a pond adjacent to a large lake, 1 from a pool (presumably seasonal) near a river, 2 from backwaters, 1 from drift beside a large river (possibly transported from elsewhere), 12 from rivers of various widths from

over 300 feet to about 25 feet, and 1 is from a roadside ditch. Aquatic vegetation was present and, except for 5 localities, was abundant or moderately abundant at all sites where living specimens were found. Bottom deposits were of various kinds but chiefly mud. Baker (1928a: 290) gives its habitat as " a mud flat or a strip of muddy beach which is kept rather moist. "

Baker (loc. cit.) has commented on the anatomy of this species. It is similar to that of *Lymnaea obrussa* (*s. str.*). The radula formula is quoted as 25-1-25, with the lateral teeth tricuspid, the intermediates (tooth 7 or teeth 7 and 8) with 3 or 4 cusps, and the marginals with 4 to 6 cusps.

Remarks: According to Baker (1911: 264, 269; 1928a: 290, 292) the short spired morph (*modicella*) and the long-spired morph (*rustica*) are sympatric, with *modicella* (*s. str.*) having the more extensive range. Baker also states (1911: 267) that: "no line can be drawn between the short and long-spired specimens, as every kind of intermediate form occurs. " Mixed lots of the *modicella* (*s. str.*) and *rustica* morphs, transititional lots, and lots which were clearly assignable to one morph or the other were collected during this survey.

It should be noted that 5 of the 7 collections from lakes are of the *rustica* morph, and the other 2 collections, although of the *modicella* (*s. str.*) morph, are rather elongate and approach the *rustica* morph. The other 7 lots of *rustica*, and 11 of the 13 lots of *modicella* (*s. str.*) are from less extensive lentic habitats or from rivers.

Burch (1959, 1960b) has demonstrated that *Lymnaea modicella* (*s. str.*) from Port Clinton, Ohio has a haploid chromosome number of 18 while *L. modicella* morph *rustica* from the Huron River at Dexter, Michigan, has 19. Obviously additional work on the taxonomic status of these morphs is required but since no mutually exclusive morphological, ecological, or zoogeographical distinctions can be made between them they are here considered as 1 species. If the chromosome differences cited prove to be the rule, however, morph *rustica* will require specific status.

Lymnaea parva Lea

Plate 22, Fig. 4; Map 55.

Lymnea parva Lea, 1841: Continuation of Mr. Lea's paper (etc.), *Proc. Amer. phil. Soc.*, *2*: 33. Type locality: "Cincinnati, Ohio."

Lymnaea sterkii Baker 1905: A new species of *Lymnaea* from Ohio (etc.). *Nautilus*, *19*(5): 51. Type locality: " Twelve miles west of Cleveland, Ohio in a small, swampy brook."

Diagnosis: Shell small to very small, lymnaeiform, with deeply incised sutures, rounded whorls, rounded aperture, and inner lip reflected over the umbilicus.

Description: Shell small (usual maximum length about $\frac{1}{3}$ inch), of moderate thickness, translucent, rather variable, with spire slightly longer than aperture in most specimens, with rounded aperture, and deeply incised sutures. Nuclear whorls satiny, about $1\frac{1}{4}$ in number, and forming a rounded apex. Whorls about 5, very convex and rounded, with deep sutures, and forming a broadly acute spire which typically is a little longer than the aperture. Aperture medium-sized, uniformly ovate or with inner lip centrally indented and continuous in many specimens. Outer lip thin and convex. Inner lip wide and reflected over the umbilicus. Umbilicus clearly defined, deep, and only partly covered by the inner lip. Sculpture consisting of crowded, fine collabral lines, irregular growth rests, and obscure spiral lines. Periostracum of medium thickness and yellowish-brown to brown.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
South Saskatchewan River, 2 mi S of Outlook, Sask.					
Length (L), mm	15	4·1 —7·5	5·68	—	—
Width (W), mm	15	2·4 —3·8	3·06	—	—
W/L	15	0·49—0·60	0·542	0·009	0·036
Ap L/L	15	0·41—0·50	0·460	0·006	0·024
Ap W/Ap L	15	0·48—0·67	0·581	0·010	0·037
Whorls	13	4·6 —5·4	5·10	—	—
Muskeg 1 mi E of Attawapiskat, Ont.					
Length (L), mm	25	3·5 —5·7	4·34	—	—
Width (W), mm	25	2·0 —3·0	2·38	—	—
W/L	25	0·48—0·63	0·552	0·007	0·035
Ap L/L	25	0·39—0·53	0·452	0·006	0·032
Ap W/Ap L	25	0·47—0·62	0·543	0·007	0·037
Whorls	24	4·2 —5·6	4·90	—	—

Records:

Eastern James Bay drainage area. Fort George River system: Fort George River, 8 mi E of Fort George, Que. (this survey). Eastmain River system: woods pool behind mission, Eastmain, Que. (this survey).

Harricanaw River system. Hannah Bay, near mouth of Harricanaw River, Que. (1904, J. Spreadborough!).

Albany River system. In forest near Kabinakagami River, 20 mi W of Hearst, Ont. Spring and woods pool, both Fort Albany, Ont. (both this survey).

Attawapiskat River system. Winonitikameg Lake, Ont. (52°23′N, 88°18′W) (1904, W. McInnes!). Attawapiskat River at entrance to large side channel around island, 6 mi W of Attawapiskat, Ont. Muskeg near Attawapiskat River, 1 mi E of Attawapiskat. Woods pool 3 mi E of Attawapiskat (all this survey).

Winisk River system. Small side channel of Winisk River, 15 mi S of Winisk, Ont. (this survey).

Severn River system. Unnamed lake at 53°37′N, 92°40′W, Ont. (in pools on flat rocks) (this survey).

Hayes River system. Stull Lake, Ont. (54°29′N, 92°37′W) (this survey).

Winnipeg River system. Pond near Falcon Lake, Man. (this survey).

Red River system. Tributary of Souris River, 2 mi S of Weyburn, Sask. city limits (this survey). Birtle, Man. (Mozley, 1938: 99).

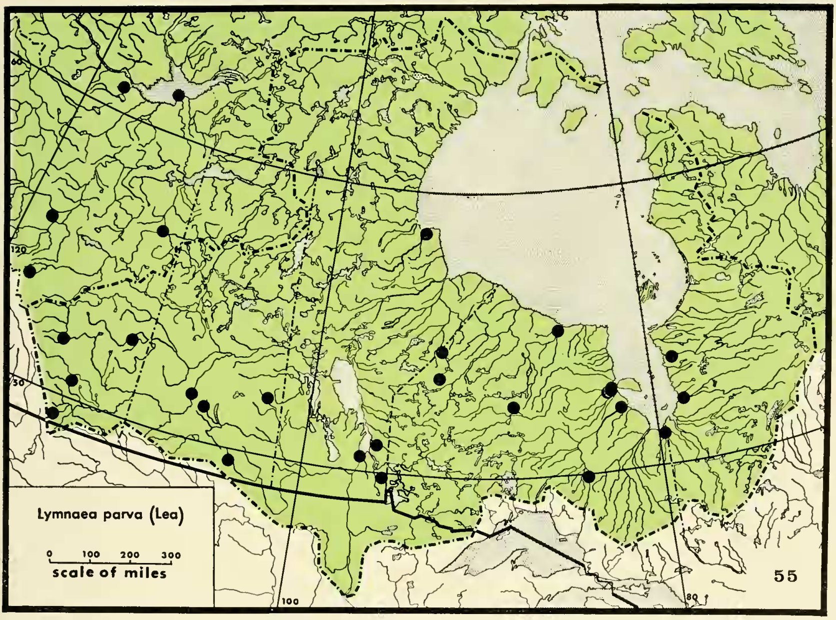
Lake Manitoba—Lake Winnipegosis drainage area. Lady Lake, Sask. (1961, D. J. Buckle!).

Saskatchewan River system. South Saskatchewan River drainage area: 1 mi E of Pincher Creek, Alta. (1966, R. Hartland-Rowe!). Chin Lake, 3 mi E of Lethbridge, Alta. Pond 12 mi S of Namaka, Alta. Waskasoo Creek, 3 mi S of Penhold, Alta. South Saskatchewan River, 2 mi S of Outlook, Sask. (all this survey). North Saskatchewan River drainage area: Pond near Whitemud Creek, W of Edmonton, Alta. (1924, L. S. Russell!). "Wainwright Park", Wainwright, Alta. (1935, W. E. Swales!). Eyehill Creek, 2 mi S of Macklin, Sask. (this survey). Saskatchewan River drainage area: Cormorant Lake, Man. (1906, W. McInnes!).

Nelson River system. O'Hanly River, 18 mi N of Pine Falls, Man. Lake Winnipeg, 20 mi S of Gimli, Man. (both this survey).

Churchill River system. Creek 65 mi S of Churchill, Man. (1929, F. Johansen!).

Mackenzie River system. Jacques Lake district, tributaries of Rocky River, Jasper National Park, Alta. (Mozley, 1938: 99). Pools near Pyramid Lake, Jasper National Park (1965, Persis and R. W. Coleman!). 6 mi SE of Hythe, Alta. (1963, F. R. Cook!). Spring, Birch Island Lumber Co., Brûlé, Alta. (this survey). 7 mi S of Mackenzie River ferry, N.W.T. [near Great Slave Lake] (1965, R. Hartland-Rowe!). Great Slave Lake, several localities (1944–46, J. G. Oughton!).



Distribution: Most of eastern North America from 36° N to James Bay (except absent from Canada east of Ontario and from most of New England), west to the Rocky Mountains and northwest to the vicinity of Great Slave Lake. In the Rocky Mountain region *Lymnaea parva* extends south to New Mexico and Arizona. (Data are from Baker, 1911 and "Records", above). Recorded from Kansan and later Pleistocene deposits in various parts of the United States (La Rocque, 1963: 12, 14, etc.)

Biology and Ecology: Twenty-two lots of *Lymnaea parva* were collected during this survey. Two lots are from drift at the edge of large mesotrophic lakes, 2 lots are from the edge of large eutrophic lakes, 5 are from (presumably) permanent woods pools, 1 large lot is from shallow pools on flat rocks at the edge of a large mesotrophic lake, 2 are from small, permanent ponds, 2 are from muskeg, 1 is from under logs near a river, 2 are from muddy river banks, 1 is from a mud flat at the edge of a river, 1 is from the flooded, grassy bank of a river, and 3 are from backwater parts of rivers. Except for the mud flat and 1 of the mud bank habitats, vegetation was thick or moderately thick at all localities. Bottom sediments were of all types but mud was observed most frequently. At least some specimens of *L. parva* occurred out of the water at 10 of the 22 collecting localities.

According to Baker (1928a: 287), this species "inhabits wet, marshy places, generally out of the water, on sticks, stones, or muddy flats. [It] is more prone to leave the water than any other species of the family." Mozley

(1938: 99) says: "It appears to prefer muddy flats on which there is little vegetation." Hoff (1937) has confirmed these observations and has described the life history of *L. parva* in detail.

The anatomy of *Lymnaea parva* has been described by Baker (1928a: 286). The radula formula given is 24-1-24. Radulae from snails collected at 7 widely spread localities visited during the present survey were examined, with the following results.

Catalogue Number	Locality	Shell Length mm	Radula Formula
29975A	Fort Albany, Ont.	3.1	19–1–19
29975B	Fort Albany, Ont.	3.5	18–1–17
40467A	6 mi W of Attawapiskat, Ont.	6.3	23–1–22
40467B	6 mi W of Attawapiskat, Ont.	5.8	23–1–22
40469A	15 mi S of Winisk, Ont.	5.3	20–1–20
40469B	15 mi S of Winisk, Ont.	5.7	22–1–21
27949	near Falcon Lake, Man.	4.2	16–1–16
40471A	12 mi S of Namaka, Alta.	5.2	19–1–19
40471B	12 mi S of Namaka, Alta.	5.8	21–1–20
32439A	Brûlé, Alta.	5.7	19–1–19
32439B	Brûlé, Alta.	5.6	20–1–19
29041A	near Coppermine River, N.W.T.	3.3	18–1–17
29041B	near Coppermine River, N.W.T.	4.6	17–1–16

Remarks: *Lymnaea parva* is quite similar to *L. bulimoides* morph *perplexa*. *L. parva*, however, has a thinner shell; a less broadly reflected inner lip; and a shorter, less acute spire. The radula of *L. bulimoides* has bicuspid 1st lateral teeth whereas in *L. parva* the 1st laterals are tricuspid.

Externally *Lymnaea bulimoides* morph *perplexa* also fits fairly well the original description *L. sterkii* Baker but the type locality of *L. sterkii* is near Cleveland, Ohio, and this is much farther east than where *L. bulimoides* occurs. It is probable that some of the literature records for *L. parva sterkii* from western Canada (e.g., Mozley, 1938: 99) actually represent *L. bulimoides* morph *perplexa*.

The status of *Lymnaea parva sterkii* is, in itself, questionable. According to the literature, the geographical ranges of the 2 "subspecies" are broadly sympatric, although *L. p. sterkii* is recorded as extending farther northward and northwestward than *L. p. parva* (Baker, 1911: 248). The type localities of both "subspecies" are in Ohio, and the described differences between the 2 taxa are of smaller magnitude than the variation accepted as normal in many polymorphic lymnaeids. In this work *L. sterkii* is considered a synonym of *L. parva*.

Prostagnicoline Nasoniaform Species

Formerly *Bakerilymnaea* Weyrauch, 1964 (= *Nasonia* F. C. Baker, preoccupied). See synonymy under *Lymnaea*.

Shells small, variable, with a blunt to pointed spire, nuclear whorls relatively large (0·5 to 0·7 mm), columella without a plait, and inner lip broad. Radula with bicuspid lateral teeth. Nasoniaform species are recorded from the Pliocene (Taylor, 1960: 22) to the Recent.

Lymnaea bulimoides (Lea)
Plate 22, Figs. 5-8; Map 56.

Lymnea bulimoides Lea, 1841: (no title) *Proc. Amer. phil. Soc., 2*: 33. Type locality: " Oregon."
Lymnea techella Haldeman, 1867: *Amer. J. Conchol., 3*: 194, pl. 6: 4. Type locality: " Texas."
Lymnaea bulimoides cockerelli Pilsbry, 1906: *Nautilus, 19*: 130; Pilsbry & Ferriss, 1906: Mollusca of the Southwestern States. *Proc. Acad. natr. Sci. Philad., 58*: 162. Type locality: " New Mexico: Las Vegas."
?*Lymnaea bulimoides sonomaensis* Hemphill, 1906: (*in*) Pilsbry & Ferriss, 1906 (op. cit.), p 162, figs. 18, 19. Type locality: " Sonoma County, California."
Galba Alberta Baker, 1919: *Bull. Amer. Mus. natr. Hist., 41*: 537, fig. 4. Type locality: " Brazean [Brazeau] Lake, Alberta, Canada."
Fossaria perplexa Baker & Henderson, 1929: *Nautilus, 42*: 103–104. Type locality: " West end Park Lake, Grand Coulee, Washington." Henderson (1929: 134) gives the original locality as " Rivulet connecting Park and Blue Lakes, Grand Coulee, Wash."

Diagnosis: Shell small, highly variable, body whorl dominant, spire acute to obtuse, and columellar area expanded.

Description: Shell small (up to about ½ inch long), highly variable, rather thin to slightly thickened, with a dominant body whorl and a spire which may be acutely pointed and " pinched " (morph *techella*), acute but not " pinched " (morphs *alberta* and *perplexa*), subacute and rather bulbous (morph *bulimoides*), (*s. str.*) or broad, rounded, and obtuse (morph *cockerelli*). Nuclear whorls smooth, satiny and brown. Whorls about 5. Sutures impressed. Body whorl inflated and dominant (especially in morph *cockerelli*). Aperture subovate. Outer lip thin at edge but thickened behind the edge by a varix which, in many specimens, is reddish-brown. Inner lip broad and extending over, but not obscuring, the umbilicus. Umbilicus plainly evident and wide or narrow. Sculpture consisting of fine collabral lines and, in some populations, also of finer spiral striae. Surface greyish-brown or brown and, in some populations, with irregular darker brown and whitish collabral streaks.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Lake 2·5 mi NW of Brock, Sask. (morph *cockerelli*).					
Length (L), mm	13	7·2 —10·8	9·17	—	—
Width (W), mm	13	4·3 — 6·8	5·62	—	—
W/L	13	0·58 — 0·65	0·613	0·006	0·020
Ap L/L	13	0·55 — 0·61	0·571	0·006	0·022
Whorls	12	4·9 — 5·5	5·27	—	—
4·4 mi S of Taber, Alta. (morph *cockerelli*, approaching morph *sonomaensis*).					
Length (L), mm	5	4·9 — 5·6	5·06	—	—
Width (W), mm	5	3·6 — 4·4	3·90	—	—
W/L	5	0·74 — 0·77	0·771	—	—
Ap L/L	5	0·58 — 0·63	0·608	—	—
Whorls	5	3·8 — 4·0	3·90	—	—
15 mi S of " Fort Chiniquay ", Alta. (morph *perplexa*).					
Length (L), mm	14	4·5 — 8·0	6·10	—	—
Width (W), mm	14	2·6 — 4·2	3·23	—	—
W/L	14	0·51 — 0·58	0·534	0·007	0·025
Ap L/L	14	0·39 — 0·48	0·419	0·006	0·024
Whorls	14	4·5 — 5·5	5·09	—	—

PLATE 22. *Lymnaea* (II)

FIG. 1. *Lymnaea decampi*, lake 20 mi E of Beardmore Ontario (NMC 40292, 8·0 mm), ... p 269.

FIG. 2. *Lymnaea exigua* (costate morph), Attawapiskat River near Attawapiskat, Ontario (NMC 29413, 8·4 mm), ... p 273.

FIG. 3. *Lymnaea modicella*, E side Lake Manitoba, Manitoba (NMC 40358, 7·3 mm), ... p 276.

FIG. 4. *Lymnaea parva*, Wainwright, Alberta (NMC 38080, 7·4 mm), ... p 279.

FIG. 5. *Lymnaea bulimoides* (*techella* morph), 19 mi W of Cayley, Alberta (NMC 40466, 10·5 mm), ... p 283.

FIG. 6. *Lymnaea bulimoides* (*perplexa* morph), ditch near Eisenhower Junction, Alberta (NMC 32423, 4·8 mm), ... p 283.

FIG. 7. *Lymnaea bulimoides* (*cockerelli* morph), 4·4 mi S of Taber, Alberta (NMC 40293, 5·5 mm), ... p 283.

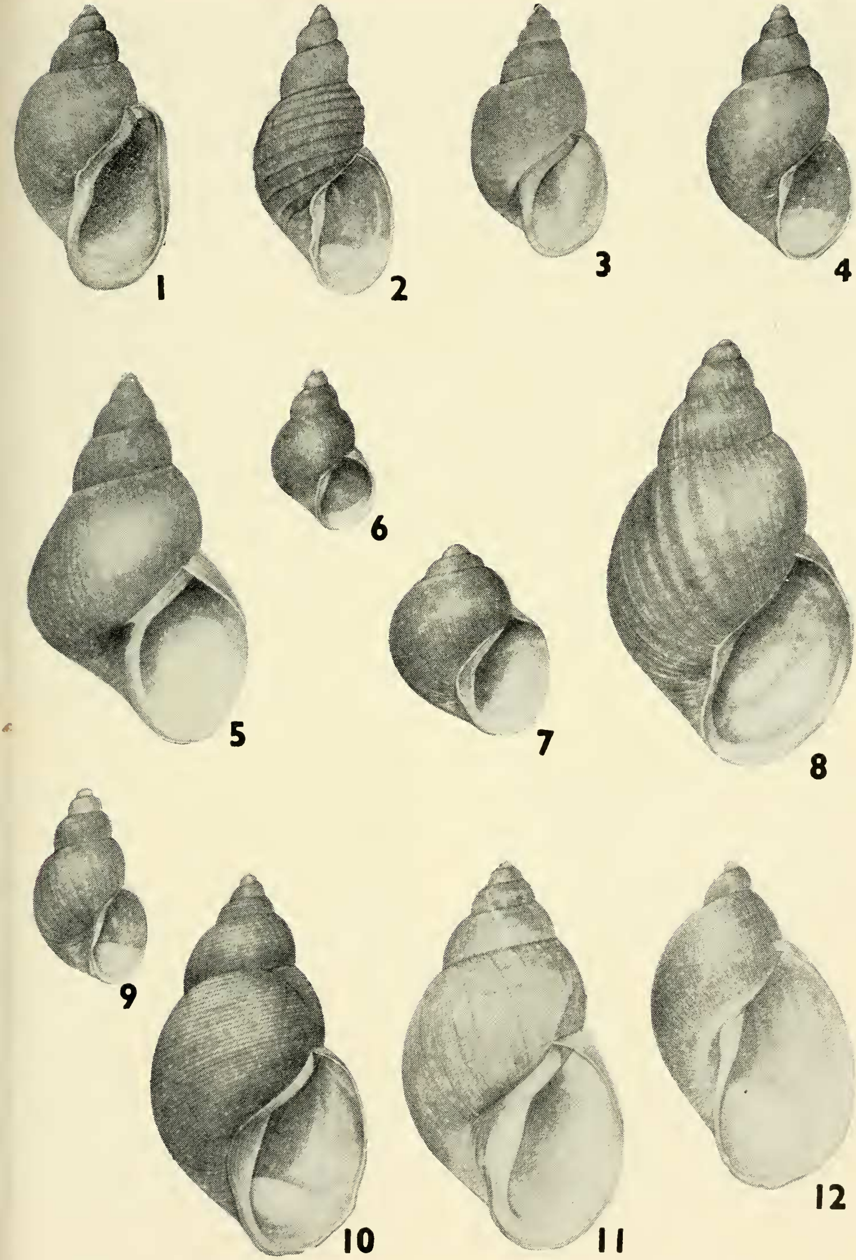
FIG. 8. *Lymnaea bulimoides* (nominate morph), Aldersyde, Alberta (NMC 38100, 11·9 mm), p 283.

FIG. 9. *Lymnaea dalli*, Trout Creek near Edston, Alberta (NMC 32578, 5·6 mm), ... p 288.

FIG. 10. *Lymnaea caperata*, 3 mi S of Carstairs, Alberta (NMC 40356, 11·0 mm), ... p 313.

FIG. 11. *Lymnaea montanensis*, 5·7 mi S of High River, Alberta (NMC 46459, 11·4 mm), ... p 317.

FIG. 12. *Lymnaea columella*, Scotia Junction, Ontario (ANSP 163896, 8·9 mm), ... p 290.



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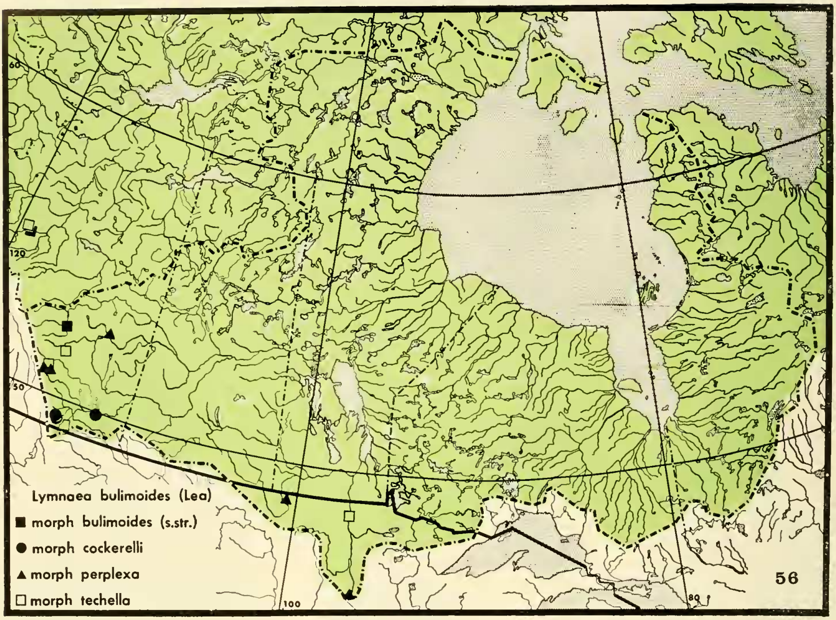


Records:

Abbreviations: (*b*), *bulimoides* nominate morph; (*c*), *cockerelli* morph; (*p*), *perplexa* morph; (*t*), *techella* morph. See "Remarks" below.

Red River system. Traverse Lake, Brown's Valley, Minn. (*p*) (in drift) (this survey).

Devil's Lake drainage area (inland drainage). Creek 12 mi W of Bottineau, N.D. (*p*) (this survey).

Saskatchewan River system. South Saskatchewan River drainage area: Ponds 15 mi SE and 5 mi E of Pincher Creek, Alta. (both *c*). 19 mi W of Cayley, Alta. (*t*) (all 1966, R. Hartland-Rowe!). Roadside ditch 1 mi SE of Eisenhower Junction, Banff National Park. Alta. (*p*) (this survey). Waterfowl Lake, Banff National Park (*p*) (1964, Persis and R. A. Coleman!). Aldersyde, Alta. (*b*) (1933, R. L. Fowler!). Small ponds 11, 12, 15, 27 and 31 mi S of " Fort Chiniquay "*, Alta. (all *p*) (all 1966, R. Hartland-Rowe!). Rosebud River, Rosedale, Alta. (*p*) (this survey). North Saskatchewan River drainage area: 1½ mi N of Rocky Mountain House, Alta. (*b*) (1963, Joyce Cook!).

Mackenzie River system. 6 mi SE of Hythe, Alta. (*c* and *t*) (1963, Joyce Cook!).

Distribution: United States west of the vicinity of the Mississippi River. Also southern Saskatchewan and Alberta (chiefly in the prairie and Rocky Mountain foothill regions) and southern British Columbia. There are no previous records of *Lymnaea bulimoides* from the Canadian Interior Basin. Fossil *L. bulimoides* have been recorded from Pliocene deposits in Kansas (La Rocque. 1963: 6, 7) and in Pleistocene deposits elsewhere in the United States within its present range.

Biology and Ecology: Only 4 collections of *Lymnaea bulimoides* were made during

* " Fort Chiniquay " is a local name associated with the Chiniquay Indian Reserve, 35 mi W of Calgary Alta.

this survey: 1 from a large, permanent lake (empty, in drift), 1 from a roadside ditch, (5 living specimens) 1 from the moist, muddy bank of a small river (1 empty specimen, in drift) and 1 from a slow-moving creek (1 living specimen). Vegetation was thick at the 2 localities where the snails occurred alive, bottom sediments were partly or wholly of mud, and the microhabitats in both cases were the same, i.e., among dense aquatic vegetation.

All 8 collections of this species made by Dr. Hartland-Rowe were also from small ponds. In 4 of these thick, emergent grass was dominant.

Several statements in the literature (e.g., Pilsbry 1896: 96) refer to the unusual ability of *Lymnaea bulimoides* to survive in habitats which are dry throughout most of the year. I have been unable to find any other published information on the ecology of the species, however.

Parts of the anatomy of *Lymnaea bulimoides* have been described by Baker (1911: 218, morph *cockerelli*; 1919: 538, morph *alberta*), and by Hubendick (1951: 129). It is apparently related to *L. cubensis* Pfeiffer, a subtropical and tropical American species. The radula formula given by Baker (1911) is 21-1-21 with 7 bicuspid laterals, 3 tricuspid transitional teeth, and 10 marginal teeth with 6 or 7 cusps. Baker (1919) gives 23-1-23 for morph *alberta*, with 10 bicuspid laterals, 2 tricuspid intermediates, and 11 marginals with 3 to 6 cusps. Specimens of *L. bulimoides* morph *cockerelli* collected during this survey near Taber, Alta. gave formulae of 24-1-23 (shell length 5·6 mm), 23-1-23 (5·0 mm) and 23-1-21 (4·9 mm), with 6 bicuspid laterals, 2 or 3 tricuspid transitionals, and the marginals with 4 to 6 cusps.

Specimens from near "Fort Chiniquay", Alta. were found to be identical with type specimens of *Fossaria perplexa* Baker & Henderson, examined at the United States National Museum. They were also examined for radular characteristics and gave the following results: 12 mi S of Fort Chiniquay, 22-1-21 (shell length 5·9 mm) and 21-1-21 (6·1 mm); 15 mi S of Fort Chiniquay, 21-1-20 (5·9 mm) and 20-1-19 (4·9 mm). The first 5 to 6 laterals are bicuspid, the next 1 to 3 are tricuspid, and the marginals have 4 or more cusps. Apparently "*F. perplexa*" is not closely related to the fossariaform lymnaeids, which all have tricuspid 1st laterals, but presumably represents a hitherto unrecognized morph of the highly variable *Lymnaea bulimoides*.

Walter (*in* Taylor, Walter & Burch, 1963: 253-4) has shown that "*Stagnicola* (*Nasonia*) *bulimoides techella*" from Texas is anatomically very similar to, and perhaps identical to, *Fossaria*, but that it has tricuspid marginal teeth of unique shape. He therefore rejects *Nasonia* (=*Bakerilymnaea*) as a discrete group. Bicuspid 1st laterals were found in 7 specimens of *Lymnaea bulimoides* collected during this survey, as cited above.

Lymnaea bulimoides has been found (Shaw & Simms, 1929) to be an intermediate host for the sheep liver fluke, *Fasciola hepatica*. Species of molluscs frequently found associated with *L. bulimoides* during this survey are *Lymnaea stagnalis* and all species of *Gyraulus*. At 2 stations *L. bulimoides* was found alone.

Remarks: Several subspecies of *Lymnaea bulimoides* have been described, with *L. b. cockerelli* supposedly the most northern. Most of these "subspecies" are recorded in Baker (1911) as having ranges which overlap broadly. Hubendick (1951: 130) was unable to find geographical trends in *L. bulimoides*

and believes that subspecific divisions were not justified. The collections made during this survey support this belief. Populations reported above under " Records " and coded on the map are given the name of the morph with which they most closely agree (see synonymy) but many lots are intermediate. One lot collected near Hythe contains both *cockerelli* and *techella* morphs, with intergrades. It is probable that *L. b. sonomaensis* Hemphill is also a morph of *L. bulimoides*. Even *L. hendersoni* Baker and *Galba bulimoides cassi* Baker (not in synonymy above, see Baker, 1911: 221, 223) may well represent morphs of *L. bulimoides* below the rank of subspecies but, since 1 or both may also be locally homogeneous populations, their status cannot be decided without much additional material. *L. dalli* Baker (compare) may also belong in this category.

It is of interest that the United States National Museum contains lots identifiable as *Lymnaea bulimoides* morph *perplexa* from localities in Montana, Utah, California, Nevada, and Arizona. Such records approximate the known distribution of other morphs of *L. bulimoides*.

Lymnaea dalli Baker
Plate 22, Fig. 9; Map 57.

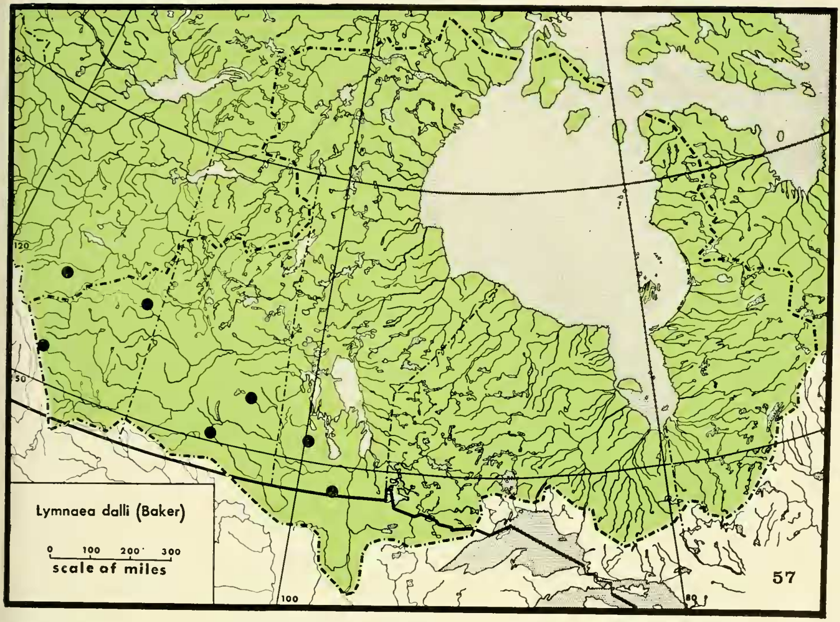
Lymnaea dalli Baker, 1907: Descriptions of new species of *Lymnaea*. *Nautilus*, *20*(11): 125. Type locality: " Lake James, Steuben Co., Indiana."

Diagnosis: Shell very small, rather thin, with convex, slightly shouldered whorls and small umbilicus.

Description: Shell very small (less than $\frac{1}{4}$ inch long), rather thin, pale brown, variable, with aperture and spire about the same length, and with convex, slightly shouldered whorls. Nuclear whorls small, brownish, satiny, and flatly rounded. Whorls $4\frac{1}{2}$ to 5, convex, roundly shouldered, and separated by deep sutures. Spire acute, with bluntly rounded apex, and a little longer than the aperture. Aperture elongate-ovate or elliptical; outer lip thin and broadly rounded; inner lip flatly reflected over the umbilical region. Umbilicus small but clearly defined. Sculpture consisting of fine collabral lines and finer, rather obscure, spiral striae.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Whitesand River, 9 mi ESE of Sheho, Sask.					
Length (L), mm	11	2·2 —4·8	3·35	—	—
Width (W), mm	11	1·5 —2·6	1·94	—	—
W/L	11	0·52 —0·68	0·583	0·015	0·049
Ap L/L	11	0·45 —0·55	0·500	0·010	0·034
Ap W/Ap L	11	0·50 —0·62	0·541	0·013	0·043
Whorls	11	3·6 —4·6	4·04	—	—
Pembina River, 6 mi N of Windygates, Man.					
Length (L), mm	7	4·3 —5·9	5·09	—	—
Width (W), mm	7	2·5 —3·2	2·83	—	—
W/L	7	0·54 —0·58	0·557	0·007	0·018
Ap L/L	7	0·51 —0·56	0·535	0·007	0·018
Ap W/Ap L	7	0·54 —0·60	0·562	0·010	0·026
Whorls	7	4·5 —5·1	4·79	—	—



Records:

Red River system. Pembina River, 6 mi N of Windygates, Man. Moose Jaw Creek, 12 mi SE of Moose Jaw, Sask. Whitesand River, 9 mi ESE of Sheho, Sask. Creek at Norland School, 8 mi ENE of Erickson, Man. (all this survey).

Saskatchewan River system. Second Vermilion Lake, Banff, Alta. Whitney Lake, southeast beach, 6 mi SE of Lindbergh, Alta. (both this survey).

Mackenzie River system. Jasper Lake [near Jasper, Alta.] (date?, Alan Mozley!). Trout Creek, 14 mi NE of Edson, Alta. (this survey).

Distribution: Great Lakes system west of Lake Ontario, Upper Mississippi-Missouri River drainage area, Canadian Interior Basin from southern Manitoba to southern Alberta, Upper Mackenzie River system in Alberta, and south in the Rocky Mountains to Arizona. Geologic range: Pliocene (Kansas and Texas) to Recent (La Rocque, 1963: 6, 7, etc.).

Biology and Ecology: *Lymnaea dalli* was found at only 7 localities during this survey. One of these is a large lake, 1 a small lake, and 5 are small rivers of 25 to 100 feet in width. Current was slow or moderate in the 4 river localities where *L. dalli* was taken alive but vegetational abundance varied widely and bottom sediments were of all types.

According to Baker (1911: 253) *Lymnaea dalli* occurs in habitats similar to those occupied by *L. parva*. Mozley (1938: 99) gives its habitat as marshes and small lakes, usually among vegetation. Data from the present survey indicate that it occurs in a variety of habitats but that, unlike *L. parva*, it is not ordinarily found out of the water or on mud flats.

No information regarding the anatomy or radula of this species is available in the literature. Two

specimens collected from the Pembina River 6 mi N of Windygates, Man. had radula formulae of 22-1-21 (shell length 5·6 mm) and 21-1-21 (4·7 mm), with the first 3 laterals bicuspid, the next 5 (transitional) teeth tricuspid and the marginals with 6 cusps.

The presence of bicuspid lateral teeth indicates a possible close kinship of *Lymnaea dalli* and *L. bulimoides*. The distributions of both species in Canada are also very similar. They have therefore been placed in adjacent systematic positions in the present work.

Prostagnicoline Pseudosuccineaform Species

Formerly *Pseudosuccinea* Baker, 1908. See synonymy under *Lymnaea*.

Shell medium-sized, succineaform, with a very large body whorl and aperture and a short spire. Radula with tricuspid lateral teeth. Known geologic range: Pleistocene (Wisconsin Period, Ohio) (La Rocque, 1963a: 32) to Recent.

Lymnaea columella (Say)
Plate 22, Fig. 12; Map 58.

Lymnaea columella Say, 1817: *J. Acad. natr. Sci. Philad.*, *1*: 14 (Binney reprint 1858: 60). Type locality not specified but presumably near Philadelphia.

Lymnaeus macrostomus Say, 1821: *J. Acad. natr. Sci. Philad.*, *2*: 170 (Binney reprint, 1858: 67). Type locality: " Cayuga Lake " [New York].

Limnaea chalybea Gould, 1840: *Amer. J. Sci.*, *38*: 196. Type locality: " Cambridge, Mass.".

?*Lymnea casta* Lea, 1841: *Proc. Amer. phil. Soc Philad.*, *2*: 33. Type locality: " Poland, Ohio".

Diagnosis: Shell medium-sized, similar to *Succinea ovalis*, with a large, ovate aperture and a moderately thin shell.

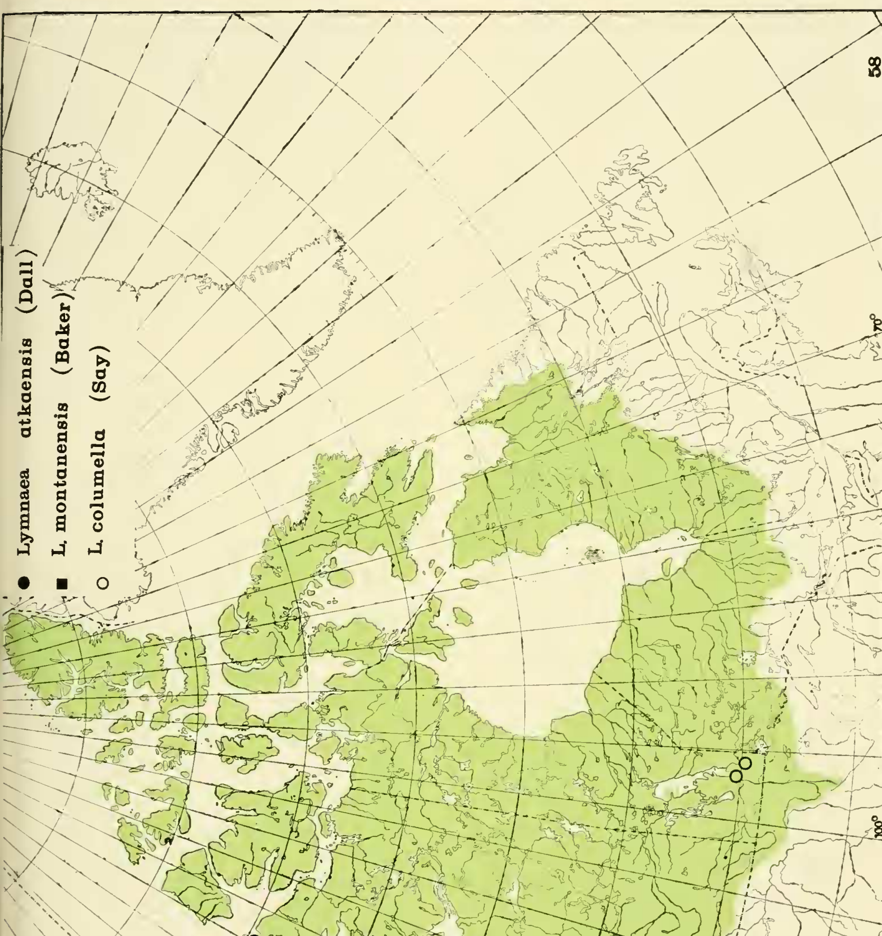
Description: Shell up to ¾ inch in length, thin and fragile to slightly thickened, light greenish-brown to yellowish-brown, variable (see " Measurements "), and with a capacious body whorl and a large, ovate aperture. Protoconch with about 1¼ whorls and forming a small and dark brown apex. Spire sharply conic, rather short and narrow, and with well-impressed and constricted sutures. Whorls about 4, rounded, but not inflated, rapidly enlarging, the body whorl comprising about ¾ of the length of the shell. Aperture ovate, expanded basally, and widely open. Outer lip thin and sharp. Inner lip closely appressed to the parietal wall and covering the umbilicus or leaving open only a narrow slit. Parietal wall arched so that in some specimens the inside of the shell is visible almost to the apex when viewed from the base. Columella plait clearly visible and gyrate, but not heavy or well developed. Sculpture consisting of moderately coarse and crowded collabral lines, darker and lighter collabral streaks, and numerous crowded spiral lines forming, in many specimens, a reticulate pattern.

Measurements:*

Feature**	N	Range	Mean	S.E.$_M$	S.D.
Georgian Bay, Lake Huron, Go Home, Ont.					
Length (L), mm	11	4·7 —11·8	7·51	—	—
W/L	11	0·47 — 0·57	0·509	0·010	0·033
Ap L/L	11	0·64 — 0·72	0·672	0·006	0·021
Ap W/Ap L	11	0·50 — 0·58	0·549	0·006	0·021
Whorls	11	2·5 — 4·2	3·57	—	—

* No population samples from the Canadian Interior Basin are available for measurement.

**No shift in ratios with increasing size was discernible. Allometry therefore appears to be negligible in this population and probably in *Lymnaea columella* as a whole.


● Lymnaea atkaensis (Dall)
■ L. montanensis (Baker)
○ L. columella (Say)

Records:

Winnipeg River system. Lake Brereton, Man. (Mozley, 1938: 97).

Nelson River system. Lake Winnipeg, Man. (Dall, 1905: 71).

Distribution: Eastern North America (east of about 100°W) from Lake Winnipeg and the St. Lawrence River system to the Gulf of Mexico. *Lymnaea columella* is very rare in the Canadian Interior Basin. Farther south the species is known from western Cuba [*L.c. francisca* (Poey)], central Mexico, Honduras, and Nicaragua (Hubendick, 1951: 133). Hubendick (loc. cit.) and Meeuse & Hubert (1949) consider the South American *L. peregrina* Clessin a synonym of *L. columella*. That species has been recorded from the region between southern Brazil and southern Argentina. *L. columella* has also been introduced to botanical gardens and ponds in Europe, South Africa, and western United States. Geologic range: Pleistocene (Wisconsin deposits in Ohio) to Recent (La Rocque, 1963: 32, 38, etc.).

Biology and Ecology: No specimens of *Lymnaea columella* were collected during this survey. Baker (1911: 170) writes that *L. columella* (*s. str.*) " is an inhabitant of ponds and streams where the water is more or less stagnant; a locality with an abundance of lily pads is particularly favourable; it is found also along the shore in shallow water in the vicinity of cat-tails (*Typha*) and other reeds, upon which it is often found mimicking the situs of the pulmonate [terrestrial] genus *Succinea*. Rarely found in running water. " Mozley (1938: 97) writes that in Lake Brereton, Man., *L. columella* " *casta* " was found " on rocky shores in shallow bays where it was somewhat protected from wave action. "

The anatomy of this species has been described by Baker (1911: 167-169; 1928a: 273-5) and by Hubendick (1951: 136). According to Baker (1911: 167) the radula formula is

$$\frac{23}{5\pm}-\frac{2}{4}-\frac{10}{3}-\frac{1}{1}-\frac{10}{3}-\frac{2}{4}-\frac{23}{5\pm}$$

(35-1-35), but no doubt some variation from this formula occurs.

Remarks: Baker (1911) recognized 2 northern subspecies of *Lymnaea columella* in addition to the nominate subspecies, viz., *L. c. chalybea* and *L. c. casta*. *L. c. chalybea* was distinguished by " its narrow shell, compressed acuminate spire, flattened body whorl and narrow and very effuse aperture. The excavated and arched columella is [a characteristic feature]. " *L. c. casta* was distinguished (from *L. c. chalybea*) by its " very narrow, elongated, somewhat oblique shell, pointed spire, long and narrow aperture, and particularly by its almost straight inner lip margin. " Although no unbiased population measurements are available, comparative dimensions of type specimens of these nominate taxa and of " *L. macrostoma*, " are of interest and are given below (from Baker, 1911).

	Length, mm	W/L	Ap L/L	Ap W/Ap L
L. columella (holotype)	22·5	0·558	0·651	0·500
L. macrostomus (holotype)	19·0	0·632	0·763	0·586
L. chalybea (syntype)	15·0	0·533	0·734	0·545
L. casta (holotype)	18·5	0·487	0·675	0·408

The *chalybea* morph occupies the same geographic area as *Lymnaea columella* (*s.str.*) in North America and cannot be considered taxonomically distinct. The *casta* morph is also sympatric with *L. columella* (*s.str.*) but is known from only the northern part of the range of that species. It is possible that *casta* may be genetically different, but no firm decision on its status can be made at present. *L. macrostomus* is considered by Baker (and by me) as a patulous abberation of *L. columella* (*s.str.*).

The shells of *Lymnaea columella* and of *Succinea ovalis* Say, a terrestrial species sometimes found in or near water, are so similar that comments on their distinguishing features are appropriate. Several authors, in fact, have confused the 2 species. *L. columella* has a small but distinct protoconch while *S. ovalis* has not. *L. columella* also bears a clearly gyrate columella and a low spiral plait. These features are absent or poorly developed in *S. ovalis*. *L. columella* is also heavier, has stronger spiral sculpture, and exhibits the same kind of apparently random inter- and intra-population variation which is characteristic of most species of *Lymnaea*. *S. ovalis* is thinner has only weak spiral sculpturing, and exhibits much less " random " variation, being similar to other land snail species in this respect. Of course, in life the animals are quite different. *Lymnaea columella* (Suborder Basommatophora) has broad, triangular tentacles with its eyes on swellings near the base of the tentacles and the surface of the head-foot region is smooth. *Succinea ovalis* (Suborder Stylommatophora) bears its eyes at the ends of long penduncles (which are wide at the base and narrow in their distal portions), the anterior or lower tentacles are reduced to small protuberances on the head near the bases of the eye penduncles and the head-foot region appears to be covered with " scales. " Many other differences of anatomy, as well as ecology, also exist; e.g., compare the anatomical descriptions of *L. columella* in Baker (1911: 167) with the descriptions of *S. ovalis* in Baker (1939a: 121) and in Pilsbry (1948: 801). Finally, although *S. ovalis* is occasionally amphibious, it is not ordinarily in the water (it is frequently found far from water) while *L. columella* always occurs in water or at its very edge.

Prostagnicoline Bulimneaform Species

Formerly *Bulimnea* Haldeman, 1841. See synonymy under *Lymnaea*.

Only 1 species has been included in this group: *Lymnaea megasoma* (Say), which see below. Radula with tricuspid lateral teeth. Recorded from the Pleistocene (Wisconsin Stage deposits, Ohio) to the Recent.

Lymnaea megasoma (Say)
Plate 12, Figs. 2, 3; Map 59.

Lymneus megasomus Say, 1824: *Major Long's Second Exped. to the Source of St. Peter's River*, etc. *2*: 263, pl. 15: 10 (Binney reprint 1858: 129, pl. 74: 10). Type locality: " Bois Blanc Lake, North-west Territory " [Basswood Lake, Ontario-Minnesota International Boundary, 48°05′N, 91°35′W, not " Manitoba " as stated by Dall, 1905: 67, Baker 1928a: 277, etc.].

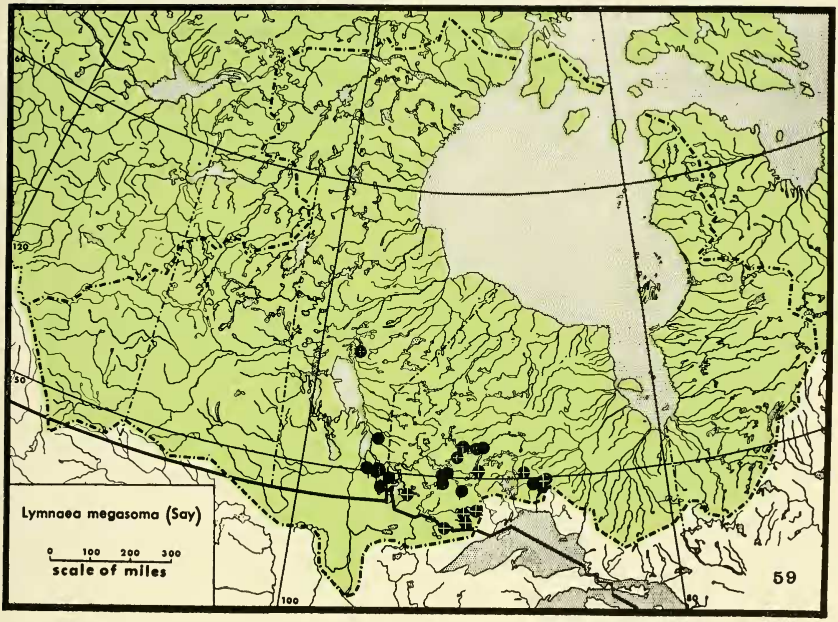
Diagnosis: Shell large, ovate, solid, and brownish or greenish; spire of medium length with convex sides; aperture large, ovate and brownish or purplish within.

Description: Shell large (up to about 1¾ inches long), relatively thick and solid, rather variable, spire of moderate length (up to the same length as the aperture, but usually less), whorls convex, and with a dominant, inflated body whorl and large aperture.

Nuclear whorls $1\frac{1}{4}$, dark brown to yellowish, and satiny. Spire conoid or cyrtoconoid (conoidal with convex sides), with rounded whorls and impressed sutures. Whorls 5 to $5\frac{1}{2}$. Body whorl broadly rounded, inflated but not bulbous, and in volume comprising most of the shell. Aperture large, acutely angled above, flatly rounded laterally, rather sharply rounded below, and chestnut brown to purplish within. Parietal wall flattened, with a gyrate plait, and a prominent callus which obscures the umbilicus completely. Periostracum slightly glossy, brownish, or greenish, and in many specimens with collabral streaks of muted green, orange, purple, or yellowish-brown. Sculpture rather coarse and composed of numerous collabral lines, low collabral ridges, and (in many specimens) numerous, irregular malleations. In many specimens the apex and early whorls are heavily corroded.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Caddy Lake, Whiteshell Provincial Park, Man.					
Length (L), mm	11	32·7 —46·7	38·3	—	—
Width (W), mm	11	21·4 —29·5	24·6	—	—
Ap L	11	20·7 —28·4	24·2	—	—
Ap W	11	10·4 —14·8	12·5	—	—
Ap L/L	11	0·608— 0·655	0·632	0·005	0·016
Whorls	10	5·5 — 6·1	5·71	—	—
Nugget Creek, 12 mi E of Dryden, Ont.					
Length (L), mm	11	29·9 —45·8	40·9	—	—
Width (W), mm	11	18·6 —27·9	24·8	—	—
Ap L	11	18·1 —28·3	24·6	—	—
Ap W	11	9·8 —14·7	13·0	—	—
Ap L/L	11	0·574— 0·631	0·603	0·005	0·018
Whorls	5	4·0 — 4·7	4·48	—	—
Medcalfe Lake, 60 mi N of Savant Lake, Ont.					
Length (L), mm	12	31·1 —45·4	39·9	—	—
Width (W), mm	12	19·5 —27·7	24·0	—	—
Ap L	12	19·2 —26·7	23·5	—	—
Ap W	12	9·7 —15·1	12·2	—	—
Ap L/L	12	0·542— 0·617	0·590	0·006	0·021
Whorls	4	4·0 — 5·0	4·60	—	—



Records:

Albany River system. Kenogamisis Lake, 7 mi SE of Geraldton, Ont. (this survey). Creek entering north end of Long Lake, [near Longlac, Ont.] (Mozley, 1938: 98). North end of Long Lake, Longlac, Ont. Wild Goose Lake, 12½ mi E of Jellicoe, Ont. (both this survey). Island in Lake St. Joseph, Ont. (1904, W. McInnes!). Marchington River, north of Drayton, Ont. (1929, A. R. Cahn!). Hill Lake, Ont. [north of Drayton] (Baker & Cahn, 1931: 54). Medium-sized lake 71 mi N of Savant Lake, Ont. Medcalfe Lake, 60 mi N of Savant Lake (both this survey).

Winnipeg River system. Rainy River drainage area: Numerous lakes in Lac des Mille Lacs swamp, Ont.; Iron Lake, St. Louis Co., Minn.; and Otterskin Lake, near Lake of the Woods, Ont. (see Baker, 1939: 93). Shoal Lake, west of Lake of the Woods, Ont. (1884, A. C. Lawson!). English River drainage area: Paguchi Lake, 7 mi N of Ignace, Ont. Nugget Creek, 12 mi E of Dryden, Ont. Inlet of small lake 3 mi W of Patricia, Ont. Pelican Lake, Sioux Lookout, Ont. (all this survey). Bamaji Lake and Cat Lake, Ont. (Baker & Cahn, 1931: 54). Several localities in Savant Lake District, Ont. (see Mozley, 1938: 94). Winnipeg River drainage area: 45 mi W of Kenora, Ont. (2 mi E of Provincial Boundary). Caddy Lake, Whiteshell, Provincial Park, Man. Whiteshell River, 1 mi N of White Lake, Man. (all 1964, Joyce Cook!). Several localities in Whiteshell River District, Man. (see Mozley, 1938: 94).

Brockenhead River system. Hazel Creek, 2 mi E of Hazel, Man. (this survey).

Nelson River system. Black River, 24 mi N of Pine Falls, Man. (this survey). Echimamish River, Man. (near 54°20′N, 97°27′W) (Bell, 1881: 75c).*

Distribution: St. Lawrence River drainage area from Lake Superior and its tributaries east to Lake Champlain,

* Incorrectly reported as "Etchimamish Lake, in Lat. 57°. [etc.]" by Dall (1905: 67) and by subsequent authors.

Vermont, and the vicinity of Montreal, Quebec (La Rocque, 1962: 29). Upper tributaries of Ohio-Mississippi River drainage area. Mahoning River, Alliance, Ohio (Sterki, 1907: 381), and numerous localities in Wisconsin, Minnesota, and Iowa (Baker, 1911: 189; 1928a: 282). Parts of the Albany, Winnipeg, and Nelson River systems in the Canadian Interior Basin (see above). Recorded from Pleistocene (Nebraskan) deposits in Nebraska (La Rocque, 1963 : 8, 9).

Biology and Ecology: Ten collections of *Lymnaea megasoma* were made during this survey. Of these 4 were from large lakes, 4 from small lakes, 1 from a river approximately 100 feet wide and 1 from ponded areas in a small creek. Vegetation was sparse to thick, bottom deposits were of all types, and in the lotic habitats the current was slow. This agrees with the observations by Mozley that the species occupies various habitats. Rush (in Baker, 1928a: 282) even reports it from a rocky lake shore exposed to constant wave action. The species most frequently occurs in muddy, heavily vegetated habitats, however.

The anatomy of this species has been described by Baker (1911: 186) and by Hubendick (1951: 82). The radula formula is quoted as $\frac{31}{5\pm} - \frac{3}{4} - \frac{14}{3} - \frac{1}{1} - \frac{14}{3} - \frac{3}{4} - \frac{31}{5\pm}$ (48-1-48) (Baker, loc. cit.). Two specimens (38 and 44 mm long) collected at Medcalfe Lake, Ont. had radula formulae of 48-1-47 and 49-1-49, respectively. In the larger specimen the 1st laterals were nearly bicuspid, the larger cusp being cleft only at the margin.

According to Rush (loc. cit.), in Georgian Bay *Lymnaea megasoma* breeds in late September and October.

Primitive Stagnicoline Lymnaeaform Species (Formae typicae)

Shells large and thin, with an elevated narrow spire, capacious body whorl, and large aperture. Radula with bicuspid or tricuspid 1st lateral teeth. Recorded from the Palaeocene to the Recent.

Lymnaea stagnalis appressa (Say)
Plate 12, Fig. 1; Map 60.

Lymneus appressus Say, 1818: *J. Acad. natr. Sci Philad.*, *2*: 168 (Binney reprint, 1858: 66) Type locality: " Inhabits Lake Superior."

" *Lymnaea stagnalis jugularis* Say " of numerous authors but probably not of Say, 1817. See " Remarks ".

?*Lymnaea stagnalis* var. *perampla* Walker, 1908: *Nautilus*, *22*(1): 8, pl. 2: 5–6. Type locality: " Houghton Lake, Roscommon County, Michigan."

Lymnaea stagnalis lillianae Baker, 1910: *Nautilus*, *23*(9): 112–113, (10): 125–126. Type locality: "Tomahawk Lake, Oneida County, Wisconsin."

Lymnaea stagnalis brunsoni Russell, 1967: *Nautilus*, *80*(4): 125–126, pl. 9. Type locality: " East shore of Flathead Lake, north of a point of land at Yellow Bay; 18 mi north of Polson, Lake County, Montana."

Diagnosis: Shell large, thin, brownish, with a tall, narrow spire, a capacious body whorl, and an ovate aperture which is approximately half as long as the entire shell.

Description: Shell large (approximately 2 inches long), thin and fragile to slightly thickened, variable, high-spired, and with a ventricose body whorl and large aperture. Nuclear whorls smooth, shining, satiny, about $1\frac{1}{2}$ in number, and forming a pointed apex. Spire narrow, acute, elongate, and composed of about 5 to 6 high, flat-sided whorls (including the nuclear whorls). Body whorl convex, rounded, inflated, and in volume comprising most of the shell. Aperture ovate, acute above, flattened axially, and convex elsewhere but variable in shape. A high proportion of specimens

in some populations exhibit a well-marked shoulder on the body whorl near the aperture, in other populations flared apertures occur, in still others the aperture is relatively narrow or relatively wide (see " Remarks "). Outer lip thin and fragile. Parietal wall covered with a thin but prominent callus. Umbilicus absent or indicated by a small chink. Columella twisted and forming a heavy, oblique, spiral plait. Surface dull to shining, relatively smooth or (in some populations) malleated, tan to dark brown, and sculptured with prominent collabral lines, prominent lines of growth, and fine spiral lines.

Measurements:

* See Charts 11 and 12 for more extensive measurements, also " Remarks ".

Feature	N	Range	Mean	$S.E._M$	S.D.
Gull Lake, Gull Lake, Alta.					
Length (L), mm	28	30·1 —43·4	37·8	—	—
Width (W), mm	28	15·3 —23·3	19·9	—	—
Ap L/L	28	0·484— 0·644	0·538	0·006	0·034
Ap W/Ap L	28	0·513— 0·681	0·571	0·008	0·037
% shouldered	28	3·6	—	—	—
% malleated	28	10·7	—	—	—
Whorls	28	5·8 — 6·8	6·49	—	—
Montreal River, Molanosa, Sask.					
Length (L), mm	26	37·1 —52·0	44·4	—	—
Width (W), mm	26	17·5 —26·1	21·7	—	—
Ap L/L	26	0·499— 0·564	0·532	0·004	0·019
Ap W/Ap L	26	0·481— 0·588	0·547	0·006	0·032
% shouldered	26	3·8	—	—	—
% malleated	26	19·2	—	—	—
Whorls	26	6·0 — 7·2	6·68	—	—
La Salle River, Elie, Man.					
Length (L), mm	30	44·0 —56·3	48·9	—	—
Width (W), mm	30	21·5 —27·0	23·8	—	—
Ap L/L	30	0·475— 0·554	0·503	0·003	0·017
Ap W/Ap L	30	0·516— 0·601	0·552	0·004	0·022
% shouldered	30	0·0	—	—	—
% malleated	30	16·0	—	—	—
Whorls	30	6·8 — 7·4	7·00	—	—

Feature	N	Range	Mean	$S.E._M$	S.D.
Nagagamisis Lake, 20 mi N of Hornepayne, Ont.					
Length (L), mm	16	37·9 —45·8	42·4	—	—
Width (W), mm	16	22·0 —28·1	24·2	—	—
Ap L/L	16	0·513— 0·589	0·558	0·005	0·021
Ap W/Ap L	16	0·506— 0·655	0·562	0·009	0·035
% shouldered	16	18·8	—	—	—
% malleated	16	100·0	—	—	—
Whorls	16	6·0 — 6·7	6·45	—	—
Hutchinson Lake, 5 mi N of Geraldton, Ont.					
Length (L), mm	20	43·2 —53·4	47·9	—	—
Width (W), mm	20	21·8 —30·6	25·1	—	—
Ap L/L	20	0·510— 0·590	0·564	0·004	0·018
Ap W/Ap L	20	0·467— 0·651	0·549	0·011	0·047
% shouldered	20	15·0	—	—	—
% malleated	20	30·0	—	—	—
Whorls	20	6·3 — 7·0	6·55	—	—

Records:

More than 210 lots of this subspecies are available from the research area so only marginal localities are cited below. All lots personally examined have been plotted on Map 60.

Southern James Bay drainage areas. Charlton Island, N.W.T. (1933, collector?). Nottaway River system: Lac Gabrielle, 10 mi S of Chibougamau, Que. Lac Doré, 10 mi SE of Chibougamau. Lake Gilman, Chibougamau (all this survey).

Harricanaw, Moose, Albany, Attawapiskat and Winisk River systems, and Shell Brook drainage area. Abundant throughout.

Severn River system, Ont. Deer Lake (52°38′N, 94°25′W) (1960, Ont. Dept. Lands and Forests!). MacDowell Lake (52°14′N, 92°47′W). Unnamed lake at 53°37′N, 92°40′W. Big Trout Lake near Post Island (53°49′N, 89°53′W). Severn Lake, south and north ends (54°00′N, 90°40′W; 54°05′N, 90°42′W) (all this survey).

Hayes River system. Stull Lake, at outlet, Ont. (54°29′N, 92°37′W) (this survey).

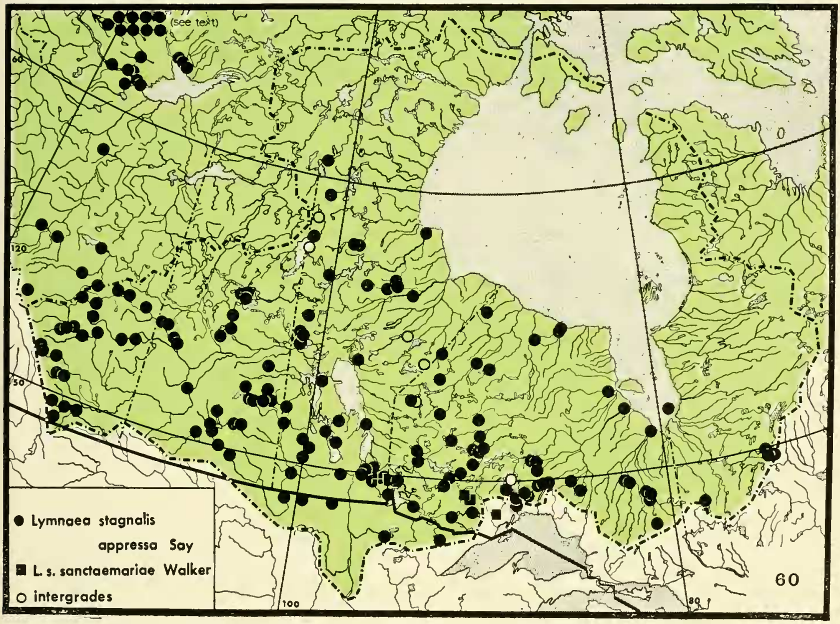
Winnipeg River system. Abundant throughout except where occupied by *Lymnaea stagnalis sanctaemariae*.

Brokenhead, Red, Saskatchewan, Nelson, Owl, and Churchill River systems; Devil's Lake, Lake Manitoba, Lake Winnipegosis, and Quill Lakes drainage areas. Abundant throughout.

Northwestern Hudson Bay drainage area. Tha-Anne River system: Kasmere Lake, Man. (59°35′N, 101°10′W) (this survey). Kazan River system: Ennadai Lake, southwest end, N.W.T. (60°45′N, 101°46′W) (this survey).

Mackenzie River system. Abundant at least as far north as Great Slave Lake and the upper Mackenzie River and vicinity. More northerly records are: Fawn Lake, Horn River, N.W.T. (62°12′N, 117°30′W) (1921, E. J. Whittaker!). Beaverlodge Lake, N.W.T. (64°42′N, 118°42′W) (1959, W. B. Scott!). Lac à Jacques, N.W.T. (66°10′N, 127°25′W). Fossil Lake, N.W.T. (66°17′N, 128°55′W) (both 1962, E. W. Innes!). Lakes 30 mi S of Aklavik, N.W.T. (1940, K. H. Lang!). Iglukitaktok, west branch of Mackenzie Delta (68°20′N, 135°26′W) (1914, J. J. O'Neill!) also cited by Johansen *in* Dall, (1919: 24a).

Distribution: *Lymnaea stagnalis* (*L.*) is circumboreal. It occurs throughout nearly all Europe, in North Africa and southwest Asia, and in a broad band across Asia to the Pacific Coast, being



apparently absent only from northern Siberia and from south-central and southeastern Asia (Hubendick, 1951: 121). In North America, *L. stagnalis appressa* (for systematic status see "Remarks") occurs throughout the Great Lakes-St. Lawrence River drainage area, northwest to the Mackenzie and Yukon River drainage areas, west to the Rocky Mountains (and possibly to the Pacific Coast—the taxonomic status of the western populations is uncertain), south in the Rocky Mountain region to Colorado and in the Mississippi-Missouri River drainage area in Illinois and Ohio. It is absent from the Hudson Bay drainage area east of northern James Bay and Hudson Bay, and from the whole Atlantic drainage area with the exception of the St. Lawrence River and its tributaries. Recorded from Sangamon deposits in Kansas and Wisconsin deposits in Ohio (La Rocque, 1963: 25, 34, etc.).

Biology and Ecology: Baker (1911: 147, 155) and Mozley (1938: 96-97) have discussed the ecology of this subspecies in some detail. Of the 141 lots collected during the present survey, 52% occured in lakes of various sizes, 9% in permanent ponds, 32% in rivers and creeks of all sizes, and 7% in other habitats (backwaters, canals, and swamps). It was not found in vernal ponds. Vegetation was present at all localities, bottom sediments were of all types (mud, sand, or rocks being most frequent) and current in lotic habitats was recorded as slow at most localities. Of course these figures reflect collecting bias, but *Lymnaea stagnalis appressa* may be considered characteristic of all permanent water bodies which support substantial vegetation.

The anatomy of *Lymnaea stagnalis* (*s. lat.*) has been described by Baker (1911: 141-144) and by Hubendick (1951: 44). Baker (1928a: 202) gives the radula formula as approximately 46-1-46 and states that the North American populations always exhibit bicuspid 1st lateral teeth, never tricuspid 1st laterals as seen in European populations. Among other details Carriker (1943) has shown that in North American populations (1) the number of radula teeth in each transverse row increases with age and size of the snails, (2) in adult snails the limits of variation in number are wide, and (3) tricuspid 1st laterals occur frequently. Tricuspid 1st laterals were also reported by Weatherburn (1964) in specimens from a pond near Ottawa, Ont.

Radulae were examined from 4 specimens collected in a lake 10 mi S of Winisk, Ontario, with the following results (all had bicuspid 1st lateral teeth):

Cat. No.	Shell length, mm	Tooth Count
40510 C	41·5	45–1–44
40510 E	40·0	43–1–42
40510 B	38·6	44–1–42
40510 D	30·3	37–1–36

Lymnaea stagnalis appressa is the intermediate host of the bird schistosome parasite *Trichbilharzia ocellata* (adult of *Cercaria elvae*), of the mammalian schistosome parasite *Schistosomatium douthitti*, and several other trematodes (Chu, 1958: 301; Malek, 1962: 64). *C. elvae* and cercaria of *S. douthitti* are among those causing cercarial dermatitis (swimmer's itch) in man.

Lymnaea stagnalis appressa is omnivorous and feeds on vascular plants, algae, rotting vegetables and fruit, and dead animals. It has even been known to attack small living fish (Baker, 1911: 147). According to Baker (loc. cit.) it breeds in the fall. Egg masses were collected during the present survey on July 14, 1962 at Clear Lake, Man.; on July 29, 1965 in Brokenhead River, Man.; on July 31, 1962 in Montreal River, Sask.; on August 8, 1967 in Abram Lake, Sioux Lookout, Ont. and on August 9, 1967 in Bamaji Lake, northern Ontario.

Remarks on *Lymnaea stagnalis jugularis* Say. Say's description of *Lymnaea jugularis* (*Nicholson's Encyclopedia*, 1st Amer. ed. 1817) also W.G. Binney (1858: 46), is unrecognizable. There is no figure and, except for the remark " in consequence of its having been found but once, [it] must be considered a doubtful inhabitant of the United States "; there is no type locality. Say's additional comment, viz., " A specimen was also brought from the West Indies by Mr. L' Heremenier of Charleston " is also entirely inappropriate for any population of *Lymnaea stagnalis*.

The next available name, *Lymneus appressus* Say, 1818, is clearly identifiable and should be used. The names *Lymnaea stagnalis jugularis* and *L.s. appressa* both occur in the recent literature and the use here of the latter name will cause no additional confusion. Whether or not the North American populations merit subspecific distinction from those in Eurasia is a

separate problem which cannot be decided at the moment.

Remarks on Inter- and Intra-population Variation. Four nominate subspecies of *Lymnaea stagnalis* have been recorded from Canada (La Rocque, 1953: 274), viz., *L.s. jugularis* Say, *L.s. lillianae* Baker, *L.s. sanctaemariae* Walker, and *L.s. wasatchensis* " Hemphill " Baker. Two other nominate subspecies, *L. s. perampla* Walker and *L.s. brunsoni* Russell have been recorded only from Michigan and Wisconsin and from Montana, respectively, but are nevertheless significant here.

The case for substituting the name *appressa* Say for the name *jugularis* Say (in the combination *Lymnaea stagnalis jugularis* Say) has been briefly discussed above. The diagnostic characters of the other "subspecies" of *Lymnaea stagnalis* from inland North America are given in the following key (adapted from Baker 1928a: 198).

1. Spire as long as, or longer than the aperture 2
   Spire shorter than the aperture 3
2. Body whorl regularly rounded, aperture acutely angled above . . . . *Lymnaea stagnalis appressa*
   Body whorl with distinct shoulder, aperture rounded above . . . . *Lymnaea stagnalis perampla*
3. Body whorl cylindrical, flattened, aperture elongate-ovate . . . . *Lymnaea stagnalis lillianae*
   Body whorl inflated, aperture expanded, roundly ovate . . . . *Lymnaea stagnalis sanctaemariae*

The 2 other " subspecies " were not included in Baker (1928a). *Lymnaea stagnalis wasatchensis* has been recorded from Utah to Washington, Alberta, and the Mackenzie River (Baker, 1911: 152) and is defined as very elongate with rounded aperture and body whorl. *L.s. brunsoni* has been recorded only from Flathead Lake in Montana and has not been defined comparatively. It appears to be close to *L.s.* " *lillianae* " in morphology, however.

In order to test the applicability and validity of these names for populations found within the study area, randomly collected population samples from various localities throughout the region were measured, classed, and analyzed statistically for all apparently significant shell characters.

The characters measured were length (L), width (W), aperture length (Ap L), and aperture width (ApW). The ratios Ap L/L and Ap W/Ap L were calculated and the number of specimens in each lot exhibiting shouldered whorls or malleated surface was tabulated. Only full-grown specimens or nearly full-grown specimens were measured or examined. In this connection it is important to note that the smaller specimens measured almost invariably gave intermediate values for the calculated ratios.

The localities of the population samples used are given below together with the number of specimens examined and the minimum, mean, and maximum length of those specimens.

Too much space would be required to report complete measurements for all 40 population samples. In order to show the extent of variation observed in typical populations, complete measurements are given for 5 such population samples under " Measurements ". The results of ratio calculations (Charts 11 and 12) are given in full because they appear to be of special significance. Qualitative observations on shouldering and on malleation show that about 3% of all lots exhibited each of these variations on at least some of the specimens contained. One scalariform specimen was also collected, with " normal " specimens, from a farm pond 6 mi SW of Abernethy, Sask.

TABLE 6. *Lymnaea stagnalis* populations analyzed statistically.

Sample No.	Locality	N	Length, mm
1	2½ mi N of Valleyview, Alta.	16	31·2–(34·0)–37·8
2	Gull Lake, 7 mi W of Lacombe, Alta.	28	30·1–(37·8)–42·7
3	Second Vermilion Lake, Banff, Alta.	8	33·1–(39·3)–46·8
4	Red Deer, Alta.	17	28·7–(31·7)–36·7
5	2 mi SE of Rosyth, Alta.	8	31·5–(37·3)–41·5
6	Turtlelake River, Turtleford, Sask.	7	35·9–(35·4)–43·3
7	Turtlelake River, Edam, Sask.	4	41·7–(48·3)–51·5
8	Sandy Lake, 20 mi S of Waskesiu, Sask.	14	23·5–(27·6)–34·4
9	Montreal River, Molanosa, Sask.	26	37·1–(44·4)–52·0
10	Slough ¾ mi W of Lady Lake, Sask.	10	36·6–(43·5)–51·0
11	Lillian River, Lady Lake, Sask.	19	23·3–(33·5)–51·2
12	Pond 6 mi SW of Abernethy, Sask.	11	32·0–(35·7)–37·5
13	Souris River, Weyburn, Sask.	19	39·4–(43·6)–48·4
14	Root Lake, 19 mi N of The Pas, Man.	13	28·0–(34·9)–41·8
15	14 mi N of The Pas, Man.	14	22·6–(27·5)–33·2
16	La Salle River, 25 mi W of Winnipeg, Man.	30	44·0–(48·9)–56·3
17	Pond 6 mi W of Whitemouth, Man.	16	23·6–(39·5)–49·8
18	Falcon Lake, southeastern Man.	30	40·8–(49·6)–59·7
19	River 12 mi W of Bottineau, N.D.	16	21·3–(29·3)–41·0
20	Gravel Lake, 6 mi NW of St. John, N.D.	9	34·8–(36·9)–40·1
21	Lower Red Lake 1 mi S of outlet, Minn.	4	21·2–(27·4)–33·6
22	Lake 71 mi N of Savant Lake, Ont.	9	31·5–(37·9)–50·1
23	Medcalfe Lake, 60 mi N of Savant Lake, Ont.	30	40·1–(44·8)–50·4
24	Pelican Lake, Sioux Lookout, Ont.	30	35·1–(42·9)–53·7
25	Sand Bar Lake, 4 mi N of Ignace, Ont.	5	47·5–(49·6)–55·0
26	Dog Lake, Thunder Bay Dist., Ont.	3	47·0–(49·8)–53·3
27	Lake 20 mi E of Beardmore, Ont.	30	40·4–(44·9)–50·0
28	Hutchinson Lake, 5 mi N of Geraldton, Ont.	20	43·2–(47·9)–53·4
29	Pond 31 mi N of Geraldton, Ont.	30	44·5–(47·2)–49·7
30	Stream at Klotz Lake, 30 mi E of Longlac, Ont.	10	40·8–(44·9)–50·5
31	Nagagamisis Lake, 20 mi N of Hornepayne, Ont.	16	37·9–(42·7)–45·8
32	Lake 10 mi E of Kapuskasing, Ont.	5	38·6–(42·9)–51·7
33	Inlet of Remi Lake, 4 mi E of Kapuskasing, Ont.	9	36·8–(41·6)–47·3
34	Long Lake, 12 mi S of Cochrane, Ont.	20	29·8–(35·4)–47·5
35	Outlet of Lake Gauvin, 4½ mi WNW of Amos, Que.	30	30·8–(37.2)–42·7
36	Lake just NE of Chibougamau, Que.	2	46·7–(51·5)–56·2
37	Reindeer Lake, Brochet, Man.	8	26·3–(30·7)–38·0
38	Limestone Lake, Man. (56°35′N, 96°00′W).	4	39·8–(45·9)–48·8
39	Muskeg 10 mi S of Winisk, Ont.	14	30·2–(37·6)–40·3
40	Yellow Creek, Fort Albany, Ont.	15	27·7–(39·8)–47·4

The measurements and observations cited above, and numerous additional observations, provide a basis for some generalizations on populations of *Lymnaea stagnalis* in this region, viz.:

1. Within the range of *L. stagnalis* (*s. lat.*) only one group of populations, i.e., populations 25 and 26, exhibit both morphological distinctness (i.e., unusually high values of Ap L/L) together with geographical unity. These populations are contiguous with similar populations in the Lake Superior region and farther north

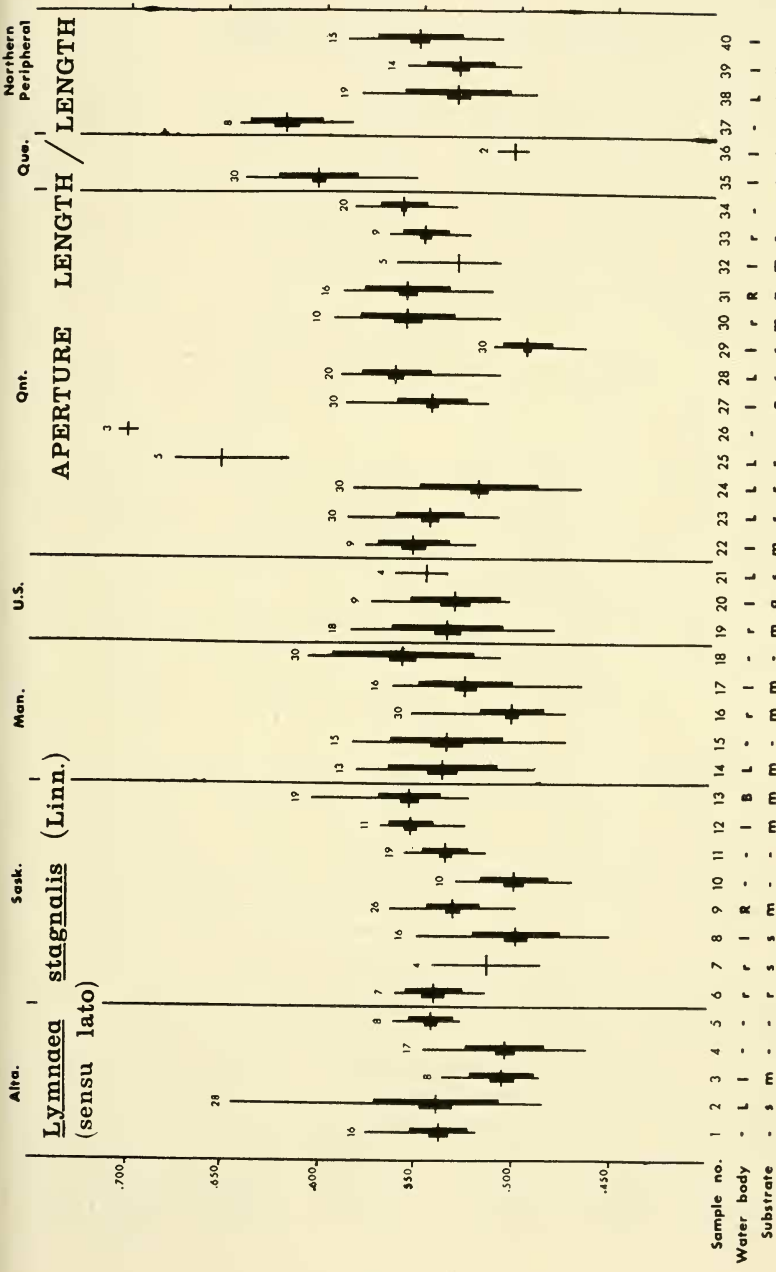


CHART 11. *Lymnaea stagnalis* populations. For explanation see p 301. Symbols are defined in caption for Chart 1.

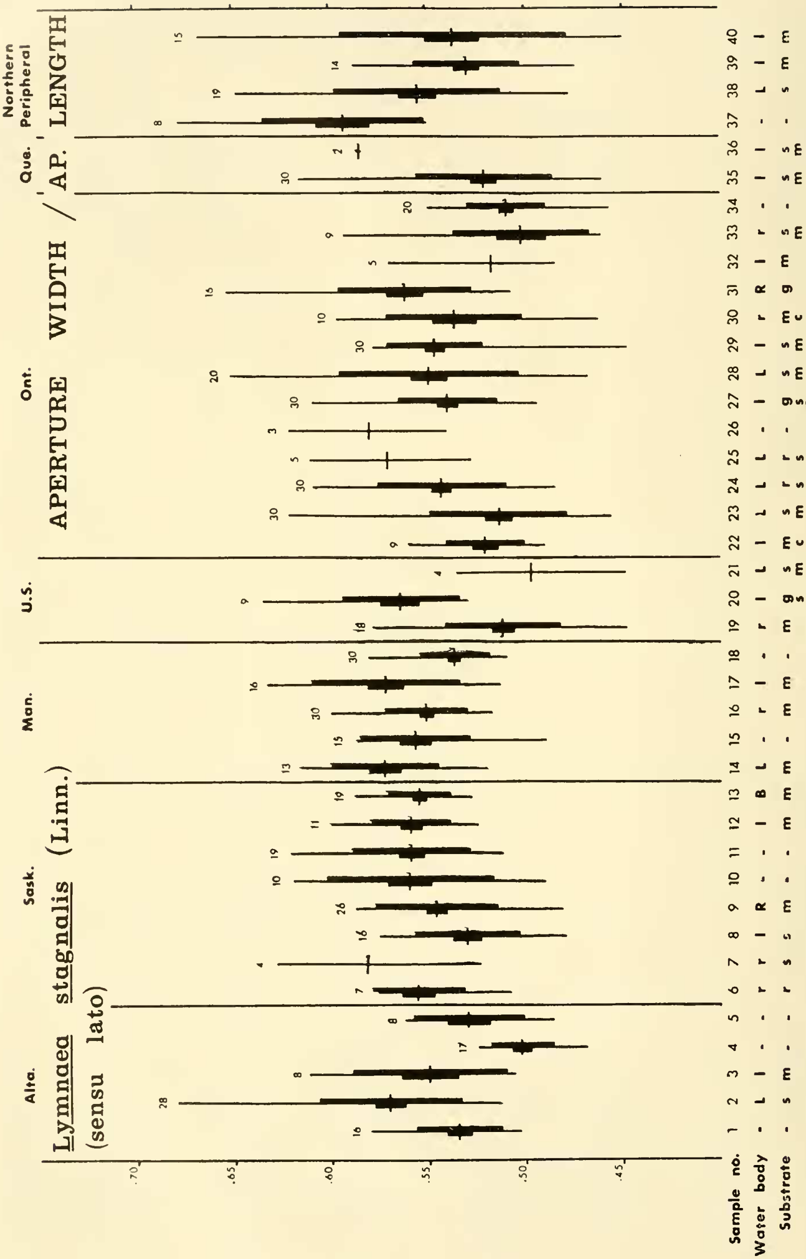


CHART 12. *Lymnaea stagnalis* populations. For explanation see 301. Symbols are defined in caption for Chart 1.

and represent a well-marked geographical sub-species, viz., *L.s. sanctaemariae* Walker, discussed on subsequent pages.

2. The chief character which has been considered diagnostic for *L.s. lillianae*, i.e., aperture length exceeding 50% of total shell length, is a commonly occurring variation in most populations of *L. stagnalis* within the region. Other characters supposedly diagnostic are also commonly occurring variations. *L.s. lillianae* is not a geographical subspecies and does not deserve separate taxonomic status. The characters distinguishing *L.s brunsoni* also appear to be common variations of *L. stagnalis.*
3. Shouldered specimens occur sporadically within many populations of *L. stagnalis* and although this character may be genetically based its expression is too diffuse to merit taxonomic distinction. Such a distribution pattern casts some doubt on the validity of *L.s. perampla* as a separate taxon, but study of the population at the type locality is needed to settle this point.
4. Some populations from western Alberta and the Mackenzie River drainage area appear to be more elongate and more cylindrical than other populations of *L. stagnalis*, and might represent subspecies *wasatchensis* " Hemphill " Baker. There also appears to be a decrease in mean values of the ratio Ap L/L with progression in a westerly direction. This decrease is not well marked, however, and it appears to be below the conventional level of subspecific distinctness. The status of *L. s. wasatchensis* cannot be judged on the basis of available evidence.
5. Surface malleation occurs in numerous populations throughout the region but does not show a geographical pattern suitable for taxonomic distinction.
6. The available data are not as extensive as might be desired but some correlations of morphology and ecology are strongly suggested. If mean values of Ap W/Ap L are compared within each separate geographical area indicated on Chart 12, the highest values always occur in habitats with sandy substrates. (Populations from the separate geographical areas, defined on the charts by vertical lines, were considered as separate groups and intra-population comparisons were made only within the same group. This reduces geographical genetic differences which might obscure ecophenotypic relationships). The only exception is in Manitoba where no samples from sandy habitats were measured. A positive correlation is also apparent between high Ap W/Ap L values and large lake habitats. Many other lots, not shown on the charts, also exhibit these correlations with substrate and habitat.

   It is of interest that the ratio Ap L/L does not correlate well with substrate. According to the literature, eg., Plaget (1929), high values of that ratio should be diagnostic of the morph called *Lymnaea stagnalis lillianae*, a morph supposedly characteristic of exposed, sandy habitats.

Lymnaea stagnalis sanctaemariae Walker
Plate 23, Fig. 1; Map 60.

Limnaea stagnalis sanctaemariae Walker, 1892: *Nautilus*, *6*(3): 31–32, pl. 1: 4–5. Type locality: " Neebish Rapids, St. Mary's River, Michigan."
Limnaea stagnalis higleyi Baker, 1905: *Nautilus*, *18*(12): 142. Type locality: " Michipicoten Bay, North Shore, Lake Superior."

Diagnosis and Description: This subspecies differs from *Lymnaea stagnalis appressa* principally in relative propor-

tions. In *L.s. sanctaemariae* the length of the aperture is approximately 65% to 70% of the length of the whole shell, whereas in most populations of *L. s. appressa* this value is only 50% to 60%. The aperture in *L.s. sanctaemariae* is also very wide and patulous, the body whorl is capacious and subglobular and the spire is short, less acute and composed of only about 4 whorls, whereas in *L.s. appressa* the spire has 5 to 6 whorls. In *L.s. sanctaemariae* the last part of the body whorl is frequently malleated or otherwise irregular. See Charts 11 and 12, " Measurements " and " Remarks. " Anatomical differences are also reported to exist.

Measurements:

Length, mm	Width, mm	Ap L	Ap W	Ap L/L	Ap W/Ap L	Whorls
Dog Lake, Thunder Bay District, Ont. (Lake Superior drainage area).						
53·3	32·7	37·0	23·0	0·694	0·621	5.3
49·0	25·4	34·5	18·6	0·705	0·540	4.8
47·0	—	33·0	—	0·702	—	5.0
Sand Bar Lake, 3½ mi N of Ignace, Ont. (English River drainage area).						
55·0	28·3	34·5	20·3	0·628	0·589	6.0
48·5	28·5	32·8	20·0	0·677	0·610	5.0
49·2	26·6	32·5	19·0	0·661	0·585	5.2
47·5	25·5	29·4	15·7	0·619	0·534	—
48·0	26·0	32·2	17·0	0·671	0·527	5.3

Records:

Winnipeg River system. Sand Bar Lake, 3½ mi N of Ignace, Ont. Paguchi Lake, 7 mi N of Ignace (both this survey). Lake Brereton, Man. (Mozley, 1938: 96, pl. 1: 9).

Distribution: Locally distributed in the Lake Superior drainage area and adjacent parts of the Lake Huron, Wisconsin River, and Winnipeg River drainage areas. *Lymnaea stagnalis appressa*-*L.s. sanctaemariae* integrades also occur in the Nipigon, Attawapiskat, Severn, Hayes, and Nelson River systems. Not recorded from Pleistocene or earlier deposits.

Biology and Ecology: Baker (1928a: 208) writes that this subspecies is " attached to the larger rocks that are not readily moved by the action of the surf. " He also cites it from an exposed lake beach, from a quiet bay (both at Isle Royale, Mich.), and from rapids in St. Mary's River. Mozley (1938: 96) gives its habitat as " large lakes, on smooth rocky shores sloping steeply into deep water in situations subject to severe wave action...The young individuals live in slightly more sheltered situations than the adults. "

During the present survey only 2 collections of this subspecies were made, and both were of empty shells from beach drift. At Sand Bar Lake (a large lake) the substrate was of rocks and sand while at Paguchi Lake (a

medium-sized lake) it was of gravel and sand. Vegetation was sparse to moderately abundant at both localities.

Baker (loc. cit.) has described the anatomy of this subspecies. It is said to differ from *Lymnaea stagnalis appressa* in details of the penial retractor muscles, in the shape of the superior jaw, and in the relative number of lateral and marginal teeth. Walter (pers. comm.) doubts the validity of these " differences ", however. Mozley (1938: 97) states that " the eggs of this variety. . . have been found in rock pools formed by the breaking of the waves on the shores, but this is probably not the usual site of egg laying. " Recently, Mozley (pers. comm., Dec. 14, 1966) has described the egg masses of Brereton Lake specimens as sausage-shaped and thicker and more solidly formed than those of *L. s. appressa*.

Remarks: Although the type locality of *Lymnaea stagnalis appressa* is " Lake Superior ", the type specimen is of the normal, attenuated morph (Baker, 1964a: 153) and may have originated elsewhere. But since both *L. s. appressa* and *L. s. sanctaemariae* occur as pure (and mixed) populations in that region, taxonomic complications are avoided.

Lymnaea stagnalis sanctaemariae has apparently evolved as a result of severe physical selection over a substantial period. Its distribution in and adjacent to Lake Superior appears to be unquestionably significant. The relatively huge aperture and short spire are both highly adaptive modifications for life in wave-exposed habitats and Lake Superior provides such an environment in extreme. Comparable adaptations are apparent in several other taxa as well (e.g., *L. s. appressa*, *L. catascopium* (*emarginata* morph), *Helisoma corpulentum* and *Anodonta grandis*). Of course large relative size of aperture is not universally related to exposed environments. *L. megasoma* and several species of Ancylidae, for example, are characteristic of heavily vegetated, protected habitats. But in many species and closely-related species groups morphological changes which are adaptive are clearly evident.

It is of interest to note that there is striking geographical concordance in the vicinity of Lake Superior of well-marked subspecies in several unrelated species groups. Attempts to correlate morphology and ecology will often be more fruitful if one considers the ecology of the area in which evolution has taken place instead of the ecology of the region where a distinctive morphological type now occurs. Obvious examples of this indirect relationship are provided by populations existing in lakes located on islands in larger lakes (e.g., *L. s. sanctaemariae* in Siskiwit Lake, Isle Royale, Lake Superior, and *Valvata sincera ontariensis* in Shakespeare Island Lake, Shakespeare Island, Lake Nipigon), populations which in all likelihood were derived from the specialized populations in the surrounding lakes. Populations in such lakes within lakes can provide evidence regarding genetic changes that may have occurred in the population now living in the surrounding lake. They can also provide a basis for assessing whether that and related populations should be accorded taxonomic distinction.

Several lakes close to and north of the region inhabited by *Lymnaea stagnalis sanctaemariae* support populations which resemble that subspecies but are not as extreme in aperture development. These populations are probably intergrades between *L.s. sanctaemariae* and *L. s. appressa*. Population samples of this intermediate type have been seen from the following localities: Nipigon River, Ont.; Lake Nipigon, Ont.;

" Ojiski " [=Ozhiski] Lake, Attawapiskat River, Ont.; O'Sullivan Lake, Ont.; Deer Lake, Ont.; Reindeer Lake, Brochet, Man.; Limestone Lake, Man.; Red Sucker Lake, Man. (54°10′N. 93°57′W); and Knee Lake, Man. (two localities). None of these intermediate populations closely approach the extreme aperture development seen in populations close to Lake Superior but all appear to be genetically related to *L. s. sanctaemariae.*

Hubendick (1951: 119) has figured extreme morphs of *Lymnaea stagnalis* from various localities in Sweden. It is clear that much inter-population variation exists throughout the whole range of *L. stagnalis* but this does not destroy the validity of *L. s. sanctaemariae* as a subspecies. It is morphologically distinct in North America and occupies a single, rather extensive, geographical region.

Stagnicoliform Species of Unknown Relationships

Shells large, relatively thin, strongly and and irregularly sculptured, and variable in shape. Radula with bicuspid and tricuspid 1st lateral teeth. Geologic range: Pleistocene (inferred) to Recent.

Lymnaea atkaensis Dall
Plate 23, Fig. 2; Map 58.

Limnaea scalaris Westerlund, 1883: Von der 'Vega'—Expedition in Asien gesammelte Binnenmollusken. *Nachrichtsbl. deut. malakozool. Ges.*, *4*: 165; Land—och Sotvatten-Mollusker insamlade under Vega-Expeditionen. *Vega-Expeditionens Vetenskapliga Iakttagelser*, *4*: 201, pl. 4: 13 (1887). Type locality: "Alaska, Port Clarence" (a bay on the Seward Peninsula, 65°12′N, 166°00′W). (Not *L. scalaris* Braun, 1853 or Sowerby, 1872).

Lymnaea ovata var. *atkaensis* Dall, 1885: Contributions to the history of the Commander Islands. No. 3.—Report on the Mollusca . . . (etc.). *Proc. U.S. Nat. Mus.*, 7: 343 (1884). Figured in Dall, 1905, pl. 2: 7, 9. Type locality: " Lake on the Island of Atka, Aleutian chain, near Korovin Bay " (Dall, 1905: 66).

Lymnaea randolphi Baker, 1905: New American lymnaeas. II. *Nautilus*, *18*(6): 63. Type locality: " Marsh Lake, near Dyea Valley, Alaska " (corrected to " Yukon Territory " by Baker, 1911: 453). [Yukon River system].

Lymnaea petersi Dall, 1905: *Land and fresh water mollusks of Alaska and adjoining regions.* Harriman Alaska Exped., *13*: 66, pl. 2: 3. Type locality: " Koyukuk River, north of the Yukon in Alaska ", [Yukon River system].

Galba alaskensis Baker, 1911: *Lymnaeidae of North and Middle America*, p 455, pl. 46: 14–15. New name for *L. scalaris* West., preoccupied.

Diagnosis: Shell moderately large, variable, umbilicate, spire acute and turreted, whorls shouldered (in most specimens), convex, and inflated, surface irregular, sutures deep, and periostracum straw-coloured and dull to shining.

Description: Shell medium to large (up to 1⅝ inches long), with up to 7 whorls, thin and moderately fragile, excessively variable, with a short to long spire and a body whorl which may be regularly enlarged, rounded, and moderate in size or bulbous, strongly shouldered, and comprising most of the shell. Nuclear whorls rough, shining, satiny, about 1½ in number, and forming a pointed apex. Spire narrow to moderately broad (spire angle varying from about 30° to 60°); scalariform, and composed of 4 to 6 strongly convex whorls. Sutures deeply impressed. Body whorl varying in relative size, irregular, malleated, shouldered in many specimens, and comprising from 70% to 90% of the total shell length. Aperture large and auriform, variable, its margin made continuous by the elevation of the inner lip which is thickened, reflected and appressed to the shell or barely touching it. Outer lip thin and convex. Umbilicus moderately wide, deep, prominent and exhibiting previous whorls except when partly obstructed by the reflected inner lip of adult specimens. Columella

twisted and sinuous in many specimens. Sculpture consisting of fine lines of growth, fine spiral lines, low spiral elevations separated by flat bands, irregular malleations, and prominent, dark growth rests. Periostracum thin, dull to shining, and straw-coloured or yellowish-brown.

Measurements:*

Feature	N	Range	Mean	S.E.$_M$	S.D.
Marsh Lake, Yukon Territory (Yukon River system).					
Length (L), mm	17	21·7 —41·9	32·0	—	—
Width (W), mm	17	15·2 —30·0	23·2	—	—
Ap L/L	17	0·533— 0·636	0·607	0·005	0·022
Ap W/Ap L	17	0·529— 0·714	0·600	—	—
% shouldered	17	82	—	—	—
% malleated	17	88	—	—	—
Whorls	14	4·6 — 5·7	5·41	—	—
Eaglehead Lake, B.C. (Liard River—Mackenzie River system).					
Length (L), mm	8	20·9 —37·2	29·8	—	—
Width (W), mm	8	13·5 —26·9	20·4	—	—
Ap L/L	8	0·574— 0·656	0·617	0·010	0·028
Ap W/Ap L	8	0·531— 0·613	0·563	0·010	0·027
% shouldered	8	62	—	—	—
% malleated	8	62	—	—	—
Whorls	4	4·5 — 5·1	4·68	—	—
Dease Lake, B.C. (Liard River—Mackenzie River system).					
Length (L), mm	30	19·2 —31·6	23·8	—	—
Width (W), mm	30	11·4 —18·9	14·4	—	—
Ap L/L	30	0·523— 0·643	0·572	0·005	0·030
Ap W/Ap L	30	0·479— 0·585	0·547	0·005	0·026
% shouldered	30	60	—	—	—
% malleated	30	97	—	—	—
Whorls	20	5·0 — 5·5	5·24	—	—
Lake near Cape Parry, N.W.T. (69°24′N, 124°33′W).					
Length (L), mm	5	23·6 —35·3	27·5	—	—
Width (W), mm	5	13·4 —20·5	16·7	—	—
Ap L/L	5	0·484— 0·583	0·513	—	—
Ap W/Ap L	5	0·576— 0·619	0·598	—	—
% shouldered	7	71	—	—	—
% malleated	7	86	—	—	—
Whorls	5	5·5 — 6·2	5·72	—	—

* See Charts 13 and 14 and " Remarks " for additional comparative data on these populations.

Records:

Northern Arctic drainage area. Lake near Cape Parry, N.W.T. (69°24′N, 124°33′W) (1962, G. Abrahamson!).

Mackenzie River system. Liard River drainage area: Dease Lake, B.C. Eaglehead Lake, B.C. (both 1962, S. D. MacDonald!). Frances Lake, Y.T. Finlayson Lake, Y.T. (both 1887, G. M. Dawson!). Mackenzie River drainage area: Fossil Lake, N.W.T. (66°17′N, 128°53′W) (1962, Fish. Res. Bd.!). 30 mi S of Aklavik, N.W.T., in lakes (1940, K. H. Lang!). Aklavik, (1957, Fish. Res. Bd.!).

Distribution: *Lymnaea atkaensis* (*Lymnaea randolphi* of authors) occurs throughout most of Alaska, including the Arctic Coastal Plain (Hanna, 1956: 7) and at least one of the Aleutian Islands (Atka Island), throughout most of the Yukon Territory (several lots from the Yukon River system have been examined), in northern British Columbia in the Liard and Yukon River systems, and east along the Arctic Coast to Cape Parry, N.W.T. The record from " Lac la Hoche " [=Lac la Hache, Fraser River System, B.C.] reported by Dall (1905: 71) is incorrect (Mozley, 1938: 104).

Biology and Ecology: Little ecological information is available for this species but, as Baker (1911: 453) has pointed out, the records show that it is characteristic of lakes.

The anatomy of this species has been studied by Walter. " It is a chimaera having marked advanced and primitive stagnicoline anatomical features, and in this it looks like a hybrid between *Lymnaea stagnalis* and *L. catascopium* " (Walter, pers. comm.).

Nothing has been published regarding the radular characters of *Lymnaea atkaensis*. In 1966, Mr. George Kellet of Whitehorse, Y. T. kindly collected and preserved a number of specimens for the National Museum of Natural Sciences from Marsh Lake, Y.T. (Yukon River system), the type locality of *L. randolphi*. The radulae of 2 specimens were examined and were as follows:

Catalogue Number	Shell Length, mm	Radula Formula
39221 A	28·5	$\frac{24}{4}-\frac{6}{3}-\frac{10}{2}-\frac{1}{3}-\frac{1}{1}-\frac{1}{3}-\frac{10}{2}-\frac{6}{3}-\frac{22}{4}$ (41–1–39)
39221 B	29·7	$\frac{26}{3\text{–}5}-\frac{6}{3}-\frac{11}{2}-\frac{1}{1}-\frac{11}{2}-\frac{6}{3}-\frac{24}{3\text{–}5}$ (43–1–41)

In specimen 39221A, most transverse tooth rows had tricuspid 1st laterals but some rows had bicuspid 1st laterals. In specimen 39221B the opposite condition prevailed.

Remarks: *Lymnaea atkaensis*, *Anodonta beringiana* Middendorf (which is not known to occur east of the Yukon River system and is not discussed in detail in this work) and a few other species are clearly glacial relicts which have survived in the Beringian Refugium (see Table 2, also Clarke, 1968). There is good supporting evidence for this conclusion. The presence of *L. atkaensis* at Cape Parry shows that the species is remarkably tolerant of arctic conditions. *L. atkaensis* also exhibits a much higher degree of morphological distinctness than any freshwater molluscan taxon which presumably evolved since the Wisconsin Glacial Stage (e.g., *Helisoma*

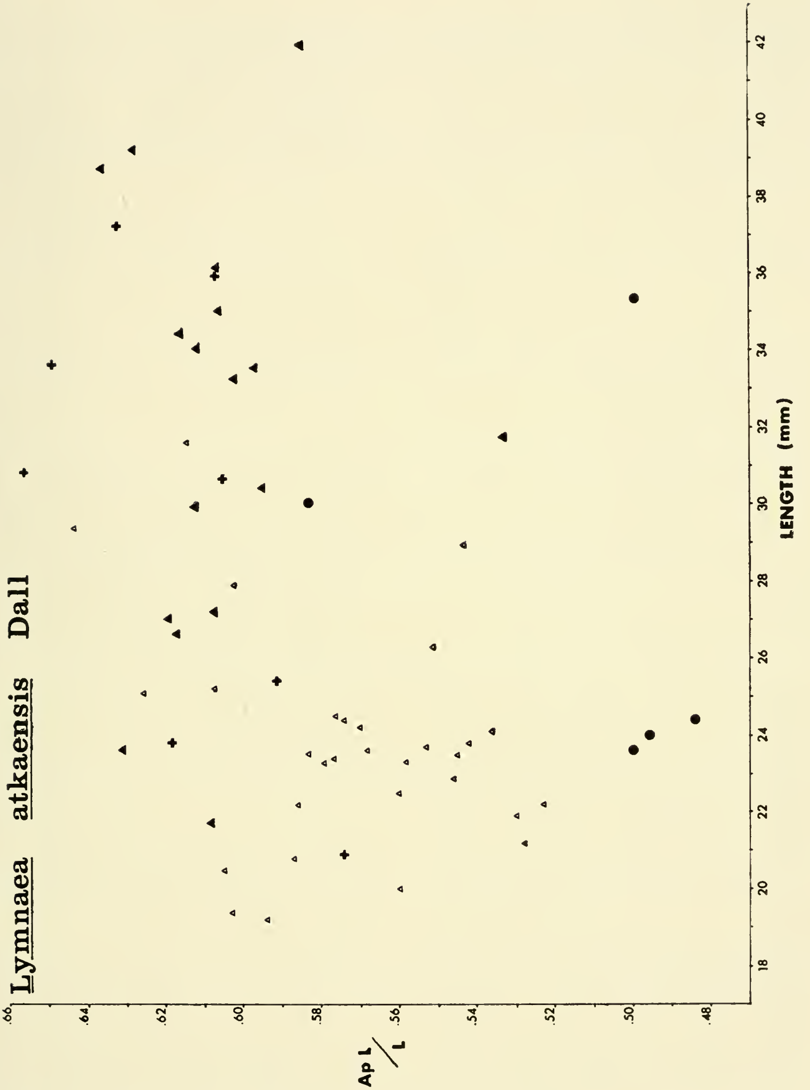


CHART 13. *Lymnaea atkaensis* populations. Symbols represent specimens from Marsh Lake (filled triangles), Eaglehead Lake (crosses), Dease Lake (open triangles) and Lake near Cape Parry (filled circles). See p 313.

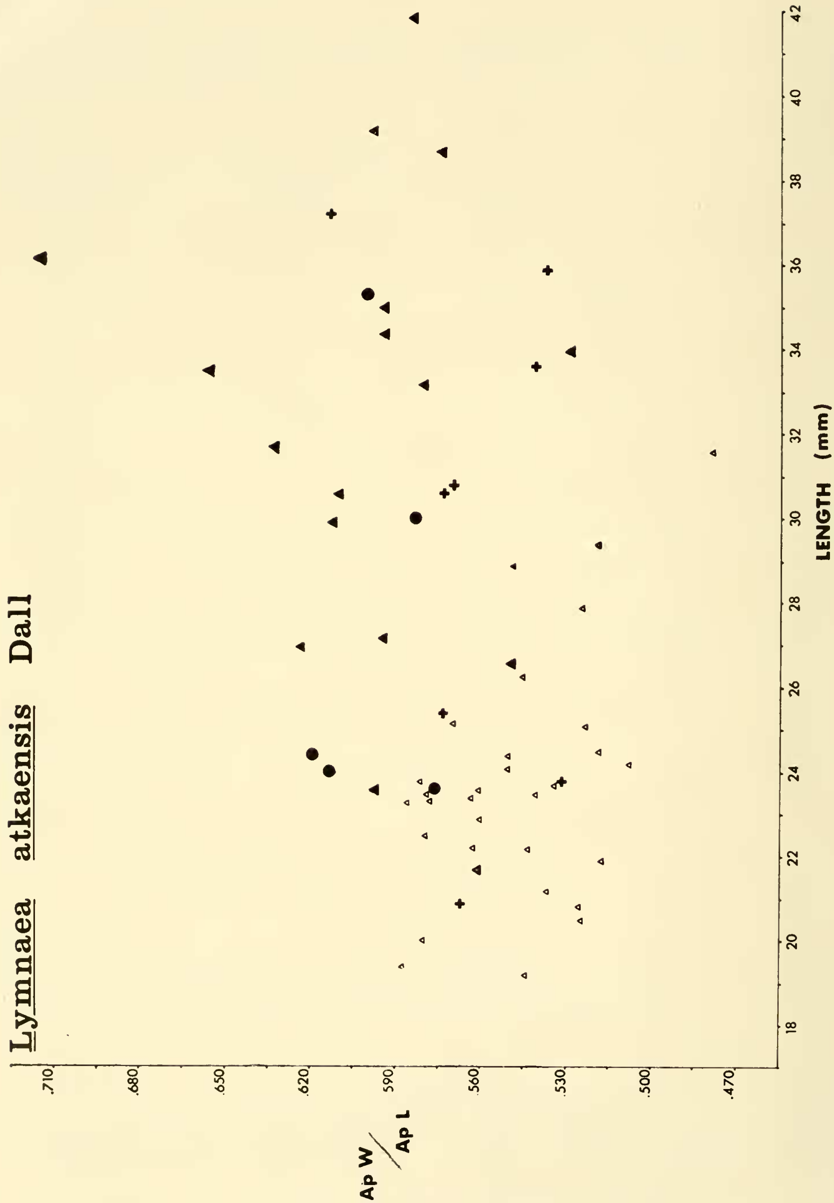


CHART 14. *Lymnaea atkaensis* populations. See Chart 13 caption for chart symbols and p 313 for explanation.

anceps royalense, *H. campanulatum collinsi*, etc.) and this is consistent with longer isolation. Finally, its distribution is unmistakably Beringian, and its expansion beyond the unglaciated region has no doubt occurred since the Wisconsin, presumably through bird transfer.

The results of comparisons between 4 population samples for Ap/L as related to L and ApW/Ap L as related to L are plotted on Charts 13 and 14 (see also " Measurements "). These characters have been considered significant by some authors for separating *Lymnaea atkaensis*, *L. randolphi*, and the other nominate forms listed in the synonymy.

Interpopulation variation in this species is obviously great. If we are to accept such variation in related species (e.g., in *Lymnaea catascopium*, *L. elodes*, etc.) as of less than taxonomic significance, and unless there are good reasons to do otherwise, we should apply the same criteria in evaluating variation in *L. atkaensis*. Type specimens of all synonyms listed were examined by the writer at the United States National Museum and all fall within the range of variation for *L. atkaensis* here demonstrated as normal.

The synonymy cited above was first suggested by Hubendick (1951: 135) and is here considered as conservative and correct. I cannot agree that *Lymnaea atkaensis* is possibly a synonym of *L. emarginata* [=*L. catascopium*], however, as also suggested by that author (loc. cit.). With the exception of the comments on the umbilicus, the differences cited by Baker (1911: 453) appear to be quite consistent, i.e., " the angularity of the whorls, the constriction of the suture, the acute spire and the deep umbilical chink easily separates it [*L. atkaensis*] from that species [*L. emarginata*]. " There are also tricuspid 1st laterals in *L. atkaensis* and none in *L. catascopium*, as demonstrated herein. Furthermore, Walter (pers. comm.) has found significant anatomical differences between the 2 species, *L. atkaensis* having both primitive and advanced stagnicoline features while *L. catascopium* has advanced features only.

Advanced Stagnicoline Hinkleyiaform Species

Formerly *Hinkleyia* Baker, 1928a. See synonymy under *Lymnaea*.

Shells small to medium-sized, with relatively large (0·5 to 0·7 mm) nuclear whorls, absent or weakly defined columella plait, and well-defined fine sculpture. Radula with bicuspid lateral teeth. Hinkleyiaform species have been recorded from the Pliocene (Taylor, 1960: 31-32) to Recent. See Taylor, Walter & Burch (1963) for additional information.

Lymnaea caperata (Say)
Plate 22, Fig 10; Map 61.

Lymnaeus caperatus Say, 1829: *N. Harmony Dissem. useful Knowl.*, 2: 230 (Binney reprint, 1858: 148). Type locality: " Indiana."

Diagnosis: Shell medium-sized to small, rather variable, relatively broad, and with numerous equidistant spiral grooves in which the periostracum stands erect forming low, fine, blade-like spiral ridges.

Description: Shell medium-sized to small (up to about 2/3 inch long), yellowish-brown, brown, or blackish, of moderate thickness, rather variable, with the aperture about the same length as the spire or slightly shorter, and with approximately 6 convex whorls separated by prominent, impressed sutures. Nuclear whorls about $1\frac{1}{3}$ in number, brown or reddish-brown, with satin-like sculpturing, and forming a narrow, subpointed apex. Spire acutely conoid or

cyrtoconoid. Body whorl inflated, dominant, and about 2/3 the length of the shell. Aperture ovate, subacute adapically, and with a thin, rounded outer lip which, in many specimens, is reinforced within by a varix which may be edged with purple. Inner lip broad, expanded over the umbilicus and without a columella plait. Umbilical chink open or partly open in most specimens. The surface of the shell under the periostracum is sculptured with numerous, fine, impressed spiral lines, fine, elevated collabral lines, and irregularly spaced lines of growth. The periostracum is dull to rather shining, closely adherent, and has fine, low, compressed, blade-like spiral ridges standing erect in the underlying grooves. This character is diagnostic of *Lymnaea caperata* and under 25x or 50x magnification it is conspicuous.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Roadside ditch 6 mi W of Whitemouth, Man.					
Length (L), mm	30	9·5 —16·3	12·88	—	—
Width (W), mm	30	5·2 — 7·3	6·04	—	—
W/L	30	0·43 — 0·55	0·472	0·004	0·024
Ap L/L	30	0·44 — 0·56	0·500	0·005	0·028
Whorls	28	5·9 — 6·7	6·16	—	—
Moose Jaw Creek, 2 mi SE of Moose Jaw, Sask.					
Length (L), mm	19	7·5 —10·4	9·22	—	—
Width (W), mm	19	4·5 — 6·1	5·19	—	—
W/L	19	0·52 — 0·60	0·564	0·006	0·026
Ap L/L	19	0·48 — 0·54	0·508	0·005	0·021
Whorls	19	5·1 — 5·6	5·35	—	—
Pond 4·5 mi E of Jenner, Alta.					
Length (L), mm	30	9·4 —12·0	10·52	—	—
Width (W), mm	30	5·7 — 7·5	6·52	—	—
W/L	30	0·59 — 0·68	0·619	0·004	0·023
Ap L/L	30	0·52 — 0·60	0·561	0·004	0·022
Whorls	29	5·0 — 5·5	5·31	—	—

Records:

Only records based on specimens personally examined are listed.

Winnipeg River system. Pond near Falcon Lake, Man. Roadside ditch 6 mi W of Whitemouth, Man. Sand Lake, 8 mi N of Virginia, Minn. (all this survey).

Brokenhead River system. Brokenhead River, 4 mi E of Vivian, Man. (this survey).

Red River system. Red River drainage area: Pembina River, 6 mi N of Windygates, Man. Stream, 6 mi SW of Oak Bluff, Man. Morris River, Brunkild, Man. (all this survey). 4·6 mi S of Stony Mountain, Man. (1960, F. R. Cook and R. A. Henry!). Assiniboine River drainage area: Souris River [=Mouse River], Mouse River Park, 15 mi WNW of Mohall, N.D. Cut Bank River, 7 mi E of Mohall, N.D. Squaw Creek, 3 mi W of Girvin, Sask. Moose Jaw Creek, 12 mi SE of Moose Jaw, Sask. Creek 4 mi E of Pense, Sask. Creek 1 mi E of Indian Head, Sask. (all this survey).

Devil's Lake drainage area (inland drainage). Rock Lake, 18 mi E of Rolla, N.D. Roadside ditch 8 mi NW of Rolla. Gravel Lake, 6 mi NW of St. John, N.D. (all this survey).

Lake Manitoba—Lake Winnipegosis drainage area. Swale, Fosston, Sask. Willow Bend Creek, 9 mi W of Portage la Prairie, Man. Lagoon at Ebb and Flow Lake, 4 mi NNW of Kinosota, Man. (all this survey).

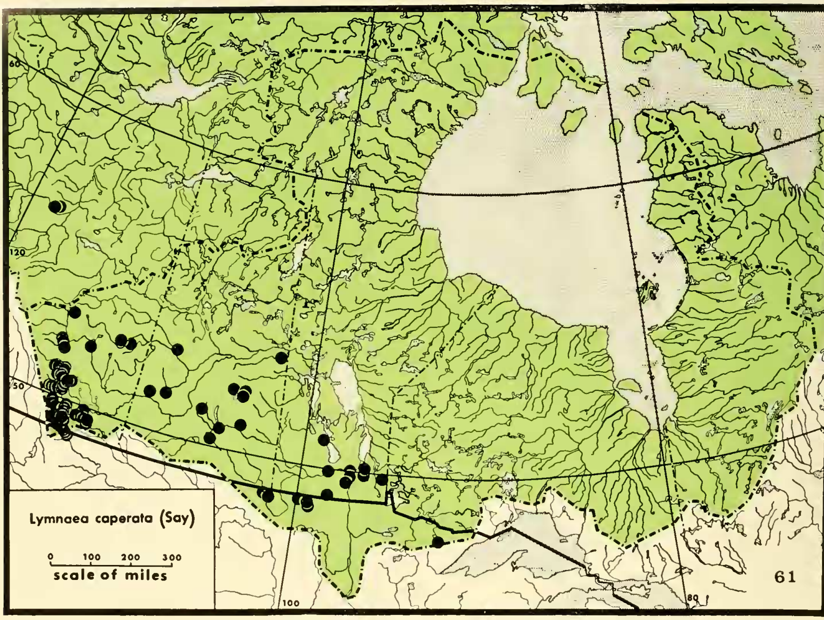
Saskatchewan inland drainage areas. Quill Lakes drainage area: Roadside ditch, Englefield (1965, D. Buckle!). Little Quill Lake (1920, McColl!). Kiyiu Lake drainage area: Lake 2½ mi NW of Brock (this survey).

Saskatchewan River system. South Saskatchewan River drainage area: Near Stirling, Alta. (2 localities). Near Wrentham, Alta. (4 localities). Near Waterton, Alta. (2 localities). Near Hill Spring, Alta. (2 localities). Brocket, Alta. 3 mi W of Mountain View, Alta. Near Pincher Creek, Alta. (13 localities). Near Cardston, Alta. (6 localities). 1 to 45 mi S of Muirhead, Alta. (11 localities). Near Fort McLeod, Alta. (3 localities). Near Cayley, Alta. (7 localities). Near Nanton, Alta. (5 localities). 22 mi S of Fort Chiniquay, Alta. Near Millarville, Alta. (3 localities). Near High River, Alta. (3 localities). Near Okotocks, Alta. (7 localities) (all 1966, R. Hartland-Rowe!). Chin Lake, 13 mi E of Lethbridge, Alta. Clear Brook, 2 mi E of Stavely, Alta. Roadside ditch 5 mi S of Carstairs, Alta. Small creek 3 mi S of Carstairs. Roadside ditch 5 mi N of Carseland, Alta. Namaka Lake, 15 mi NE of Carseland. Pond 12 mi S of Namaka, Alta. Eagle Lake slough, 3 mi SE of Strathmore, Alta. Pond 11 mi WSW of Pollockville, Alta. Pond 4½ mi E of Kenner, Alta. Waskasoo Creek, 3 mi S of Penhold, Alta. (all this survey). North Saskatchewan River drainage area: Pond 1 mi E of Lindbrook, Alta. Opuntia Lake, 3 mi ENE of Plenty, Sask. Jackfish River, 1 mi NW of Prince, Sask. (all this survey). Saskatchewan River drainage area: Pond near Carrot River, about 50 mi SW of The Pas, Man. (this survey).

Mackenzie River system. South Fork, Rings Creek, 5 mi SW of Fairview, Alta. Leith River [=Little Burnt River], 2 mi NNW of Whitelaw, Alta. (both this survey). Pond 7 mi S of Mackenzie River (about 50 mi WNW of Hay River), N.W.T. (1965, R. Hartland-Rowe!).

Distribution: According to Baker (1928a: 263) *Lymnaea caperata* ranges "from Quebec and Massachusetts west to California; Yukon Territory and James Bay south to Maryland, Indiana, Colorado, and California." It is also recorded from Alaska (Baker, 1911: 233). During the present survey undoubted *L. caperata* was seen only from the prairie states and provinces and the range given by Baker may be too extensive. Its occurrence in Montana, Idaho, Nevada, Wyoming, and Utah is documented by Taylor, Walter, and Burch (1963: 261-264) but Baker's far northern and far eastern records are probably incorrect. Fossil specimens of *L. caperata* are recorded from the Pliocene of Kansas (Taylor 1960: 31-32) and from Pleistocene deposits elsewhere (La Rocque, 1963: 8, 10, etc.).

Biology and Ecology: Thirty-six collections of living *Lymnaea caperata* were made during this survey. Twenty-five lots are from seasonal water bodies of diverse types, i.e., 1 is from a large, shallow prairie lake, 6 are from shallow ponds, 4 are from roadside ditches, 3 are from sloughs, 2 are from swamps, and 9 are from intermittent streams. Eleven lots are from flooded or otherwise shallow parts of perennial water bodies, but water bodies which undoubtedly diminish during dry periods so that the shallow parts become dry. Four of these localities are large lakes, 1 is a small lake, 2 are ponds, and 4



are rivers and streams whose widths are approximately 300, 50, 30, and 25 feet respectively. Aquatic vegetation or flooded grass was noted at all localities and was abundant at slightly over half. Bottom sediments were of mud at nearly all localities and the current was moderate, slow, or not discernible at all stream sites.

Taylor *et al.* (1963: 266) give the habitat of *Lymnaea caperata* as " found most often in seasonal bodies of water. It is characteristic of such habitats as irrigation ditches, sloughs, and shallow ponds. Its wide distribution is correlated with its tolerance for environments in which few other snails live, and with the common and widespread occurrence of habitable situations." Mozley (1938: 98) writes " usually in temporary ponds, but sometimes to be found in marshes...a common species on the prairies and parkland [but] somewhat less abundant in the forested region. "

The records resulting from the present survey confirm these observations and extend them to include flooded or otherwise shallow marginal parts of perennial water bodies, the marginal parts of which become dry, at least in part, during the year.

The anatomy of *Lymnaea caperata* has been described by Baker (1911: 229-231; 1928a: 261-3) but its distinctive features were first clearly expressed by Walter (*in* Taylor, Walter & Burch, 1963: 254).

The radula formula given by Baker (1928a) is $\frac{20}{5\text{–}7} - \frac{4}{3\text{–}4} - \frac{8}{2} \quad \frac{1}{1} - \frac{8}{2} - \frac{4}{3\text{–}4} - \frac{20}{5\text{–}7}$ (32-1-32).

Radulae were extracted from 4 specimens collected from a roadside ditch 6 mi W of Whitemouth, Man. with the following results:

Catalogue Number	Shell Length, mm	Radula Formula
32242 A	11·2	$\frac{19}{4\text{–}6}-\frac{2}{3}-\frac{7}{2}-\frac{1}{1}-\frac{7}{2}-\frac{2}{3}-\frac{19}{4\text{–}6}$ (28–1–28)
32242 B	11·6	$\frac{22}{4\text{–}8}-\frac{1}{3}-\frac{6}{2}-\frac{1}{1}-\frac{6}{2}-\frac{1}{3}-\frac{22}{4\text{–}8}$ (29–1–29)
29240 A	15·3	$\frac{21}{4\text{–}6}-\frac{5}{3}-\frac{9}{2}-\frac{1}{1}-\frac{9}{2}-\frac{5}{3}-\frac{18}{4\text{–}6}$ (35–1–32)
29240 B	15·4	$\frac{18}{4\text{–}5}-\frac{3}{3}-\frac{9}{2}-\frac{1}{1}-\frac{9}{2}-\frac{3}{3}-\frac{17}{4\text{–}5}$ (30–1–29)

In specimen 32242B some variation between tooth rows was seen, cusps on the 3rd to 6th lateral teeth being bifurcate or trifurcate in some rows and uncleft in other rows. Clearly much variation in the radula formulae of *Lymnaea caperata* exists and this cannot be expressed by a single formula.

Lymnaea montanensis (Baker)
Plate 22, Fig. 11; Map 58.

Galba montanensis Baker, 1913: A new Lymnaea from Montana. *Nautilus*, *26*(10) : 115. Type locality: " Hayes Creek, near Ward, Montana, in the Bitter Root Mountains, altitude 3825 feet" [probably Hays Creek, about 3 miles south of Ward Mountain, Ravalli County, Montana in about S ½ sec. 3, T.4N., R.21W (Taylor, *et. al.* 1963: 240)].

Diagnosis: Shell medium-sized to small, rather variable, moderately broad, with convex whorls, a distinctly shiny periostracum, and in most specimens there are irregular collabral lines and numerous spiral rows of tiny crescents.

Description: Shell up to about 3/5 inch long, brownish, of moderate thickness, rather variable, with the aperture a little shorter in length than the spire and with about 6 convex whorls separated by prominent, impressed sutures. Nuclear whorls about $1\frac{1}{3}$ in number, brown or reddish-brown and forming a blunt apex. Spire acutely conoid or cyrtoconoid. All whorls convex and inflated, the body whorl being about $\frac{2}{3}$ as long as the whole shell. Aperture relatively small, elongate-ovate, with a rounded outer lip and a rather straight, oblique columellar lip which is often angled where it is appressed to the preceding whorl. Columellar lip broadly reflected, sub-triangular, and exposing a small but definite umbilicus. Columellar fold absent or poorly defined. Periostracum shiny and closely adherent. Sculpturing consists of spirally arranged rows of tiny, crescent-shaped ridges whose ends point away from the aperture and numerous, irregularly-spaced collabral lines. The crescents may be poorly defined or fairly obvious (under 25x magnification) but some crescents are usually discernible on all specimens.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Cottonwood Creek, Franklin Co., Idaho.*					
Length (L), mm	21	8·1 —14·6	9·68	—	—
W/L	21	0·40— 0·51	0·457	0·006	0·029
Ap L/L	21	0·37— 0·44	0·404	0·005	0·021
Ap W/Ap L	21	0·55— 0·68	0·625	0·009	0·040
Whorls	21	5·3 — 6·5	5·8	—	—
Driggs, Teton Co., Idaho.*					
Length (L), mm	22	10·0 —14·6	11·88	—	—
W/L	22	0·46— 0·54	0·500	0·005	0·024
Ap/L/L	22	0·41— 0·49	0·443	0·005	0·023
Ap W/Ap L	22	0·56— 0·67	0·612	0·005	0·024
Whorls	22	5·8 — 6·3	5·9	—	—
5.7 mi S of High River, Alta.					
Length (L), mm	1	11·4	—	—	—
W/L	1	0·544	—	—	—
Ap L/L	1	0·500	—	—	—
Ap W/Ap L	1	0·509	—	—	—
Whorls	1	5·7	—	—	—

* Adapted from data in Taylor, *et al.* (1963: 244–245).

Records:

Saskatchewan River system. 5·7 mi S of High River, Alta., near highway 2A (June 10, 1966, R. Hartland-Rowe!). Only one specimen, empty but fresh, was found.

Distribution: Rocky mountain region from southern Alberta through Idaho, western Montana, western Wyoming, Utah, and Nevada. Also recorded (Taylor *et al.* 1963: 260) from a Pliocene deposit in Wyoming and from several late Pleistocene deposits in Idaho.

Biology and Ecology: According to Taylor, *et al.* (1963: 267) *Lymnaea montanensis* occurs in clear mountain streams and in small to very small pools, sometimes only a few inches wide, kept fresh by seepage or by springs. The Alberta specimen was found in the Rocky Mountain foothills in a roadside ditch about 100 feet long, 10 feet wide, and 7 inches deep. The water was clear, yellow-brown in colour, and filled with dense, emergent grass.

The anatomy of this species has been discussed by Walter (*in*) Taylor, *et al.* (1963: 247-253). It is similar to that of *Lymnaea caperata.* Burch (*in* Taylor *et al.* 1963: 255-258) has described the chromosomes and other cytological details of spermatogenesis of this species. The haploid chromosome number is 18, in common with nearly all other

prostagnicoline and stagnicoline species and subspecies of *Lymnaea* so far investigated. The radula reported by Walter (loc. cit.) was from a snail with a shell 8·1 mm long, and had the formula 28-1-32. It was similar in general to advanced stagnicoline species of stagnicolaform *Lymnaea*.

Remarks: In the hinkleyiaform lymnaeids crescentric sculpturing is an important character for the identification of *Lymnaea montanensis*. Crescents also occur in *Lymnaea elodes*, *Physa gyrina*, and in several other gastropod species, however, and in these species they are often even more prominent than on *L. montanensis*. The shiny periostracum, prominently rounded whorls, deep sutures, and relatively small aperture (Ap L/L $<0{\cdot}500$) of *L. montanensis* will distinguish the shell of that species from crescentrically sculptured shells of *L. elodes*, however. *L. elodes* has a dull periostracum, flatly rounded whorls, shallower sutures, and a relatively larger aperture (Ap L/L $> 0{\cdot}500$). Other species with crescentric sculpturing differ from *L. montanensis* by other, more obvious characters and they cannot be confused with it.

Advanced stagnicoline stagnicoliform species

Formerly (but incorrectly) *Stagnicola* Leach (*in*) Jeffreys, 1833. See synonymy under *Lymnaea* and "Remarks" under *L. elodes* (p 354).

Shells medium-sized to large, variable within and between species, and in many species with a broad parietal lip and with or without a columella plait. Nuclear whorls medium to large (0·55 to 0·70 mm). Radula with bicuspid lateral teeth.

The number of species of stagnicoliform *Lymnaea* is unsettled (see "Remarks" under *L. elodes*). The geologic range of "stagnicoliform" snails is reported as Upper Cretaceous (Zilch, 1959: 93) to Recent.

Lymnaea arctica Lea
Plate 12, Figs. 4-6; Map 62.

Lymnaea arctica Lea, 1864: *Proc. Acad. natr. Sci. Philad.*, p 113; 1866: *J. Acad. natr. Sci. Philad.*, *6*: 160, pl. 24: 75. Type locality: "Moose River, of Hudson's Bay, Arctic America."

Diagnosis: Shell similar to *Lymnaea elodes* except smaller, with heavier columella development, and in many specimens with a proportionately larger body whorl and a thicker, more prominent columella plait.

Description: Shell up to $\frac{3}{4}$ inch high, unusually variable, rather heavy, pale brown to blackish, spire of medium height, with a heavy columella callus and a dominant body whorl. Nuclear whorls about $1\frac{1}{2}$ in number, rounded, shiny, and yellowish-brown to reddish-brown. Whorls rounded, about 6 in number, and forming an acute, medium-sized spire with impressed sutures. Spire whorls wider than high. Body whorl convex but not inflated and occupying about $\frac{3}{4}$ the length of the shell. Aperture subovate, about half the length of the shell and in many specimens, purplish-brown within. Outer lip convex, sharp, and in some specimens thickened internally by a varix. Inner lip broad, thick, expanded over the umbilicus and obscuring it in many specimens. Columella plait variously developed, i.e., heavy, moderate, or absent. Sculpturing variable and consisting of numerous weak to strong collabral lines and, in many specimens, weak to strong spiral ridges, bands, or malleations, or any combination of these. Fine sculpture normally composed of tiny crescents between the spiral lines, the ends of the crescents pointing away from the aperture (as in *Lymnaea elodes*, *L. montanensis*, etc.). Periostracum closely adherent, shining, and yellowish-brown to blackish-brown.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Moose River, Moose Factory, Ont. (type locality of *L. arctica*).					
Length (L), mm	30	11·9 —17·3	14·61	—	—
W/L	30	0·50— 0·63	0·561	0·005	0·029
Ap L/L	30	0·47— 0·59	0·535	0·005	0·027
Ap W/Ap L	30	0·46— 0·55	0·508	0·004	0·023
Whorls	30	5·1 — 5·9	5·55	—	—
Lake, Mowat Island, Nastapoka Islands, Hudson Bay.					
Length (L), mm	30	16·1 —22·3	18·58	—	—
W/L	30	0·45— 0·55	0·492	0·004	0·022
Ap L/L	30	0·41— 0·52	0·470	0·005	0·028
Ap W/Ap L	30	0·44— 0·52	0·484	0·005	0·027
Whorls	30	6·0 — 6·7	6·36	—	—
Ennadai Lake, south end, N.W.T.					
Length (L), mm	30	14·1 —20·9	16·84	—	—
W/L	30	0·46— 0·58	0·515	0·005	0·030
Ap L/L	30	0·41— 0·57	0·495	0·006	0·035
Ap W/Ap L	30	0·44— 0·56	0·496	0·005	0·028
Whorls	17	5·0 — 6·5	5·59	—	—

Records:

Code numbers refer to morphological characters. See " Remarks ".

Northeast Hudson Bay drainage area. Lake, 2 mi N of Inoucdjouac (Port Harrison), Que. (Innuksuak River system) (0·53–2–2). Lake, north-central Broughton I., Nastapoka Islands, N.W.T. (0·50–2–3). Lake, southern Mowat I, Nastapoka Islands (0·46–2–3) (all this survey).

Southeast Hudson Bay drainage area. Pond, north-central Anderson I., Nastapoka Islands, N.W.T. (0·50–1·5–3). Char Lake and Lower Char Lake, west side of Richmond Gulf, Que. (0·54–1·5–3). Lake $\frac{1}{2}$ mi N of Deer River and 4 mi from Deer River mouth, west side of Richmond Gulf (0·50–2–3). Middle Fork, Roggan River, 73 mi SSW of Poste de la Baleine (Great Whale River), Que. (0·50–1–3) (all this survey). Pond on limestone island N of Cape Jones, E coast Hudson Bay (0·50–2–3). Little Whale River, Que. (0·50–2–3). Poste de la Baleine (Great Whale River), Que. (0·50–2–1) (all 1920, F. Johansen!). Kasegalik Lake (0·50–2–2) and Kapasilik Lake (0·50–2–3), Belcher Islands, N.W.T. (both 1959, M. Freeman!). Fort George River, 11 mi E (0·55–1–3), and 17 mi E (0·52–1·5–2) of Fort George, Que. Eastmain River, 16 mi E (0·50–2–3) and 1 mi E (0·60–2–2) of Eastmain, Que. (all this survey). Trout pond, S side of Charlton I., James Bay, (0·50–2–3) (1920, F. Johansen!). Salt Water Lake, Charlton I. (0·46–2–3) (1933, H. G. Richards!). Hannah Bay, Southern James Bay (0·50–2–2) (1904, W. Spreadborough!).

Moose River system. Ditches and pools along railroad, etc., Moosonee, Ont. (0·50–3–2) Moose River, beach at Moosonee (0·53–2–3). Moose River, Moose Factory, Ont. (type locality of *L. arctica*) (0·56–2–2) (all this survey). Shipsands Island mouth of Moose River

(0·50–2–2) (1933, H. G. Richards; 1953, J. L. Chamberlin!).

Albany River system. Small ox-bow lake next to Devil's Gut, S of Albany Island, Albany River estuary (0·50–2–1). Marsh, S side of Albany Island (06·0–2–2). S shore of Albany River near mouth (0·50–2–3). Albany Island, E end, at James Bay (in tidewater) (0·50–2–3) (all this survey).

Attawapiskat River system. Monument Channel at portage to Attawapiskat River, 20 mi W of Attawapiskat, Ont. (0·56–2–3). N side of Attawapiskat River, 3 mi E of Attawapiskat (0·50–2–3) (both this survey).

Winisk River system. Muskeg ditches, Winisk, Ont. (0·50–2–2). Ponds in marsh 6 mi E of Winisk (0·50–1–3) (both this survey).

Owl River system. Owl Lake, Man. (56°22′N. 94°35′W) (0·50–2–3) (this survey).

Churchill River system. Goose Creek, at mouth and ½ mi up from mouth, both 7 mi S of Churchill, Man. (0·50–2–3). Landing Lake, near Churchill (0·53–1·5–3). Partly dry muskeg behind Hudson Motel, Churchill (0·50–2–3) (all this survey). Tundra pools, Fort Churchill, Man. (0·50–2–3) (1929, F. Johansen!).

Western Hudson Bay drainage areas. South Knife River system: South Knife River (58°28′N, 95°38′W) (0·55–2–3) (1967, B. C. McDonald!). Caribou River system: Long Lake, E end (59°24′N, 95°18′W) (0·48–1·5–2) (this survey). Thlewiaza River system: unnamed lake in Thlewiaza River, N.W.T. (60°23′N, 95°45′W) (0·50–1·5–3). Tha-Anne River system: South Henik Lake, N.W.T. (61°30′N, 97°25′W) (0·56–1·5–3) (all this survey). Hyde Lake, N.W.T. (60°45′N, 95°22′W) (0·56–1·5–3) (1959, Fish. Res. Bd.!). Kazan River system: Ennadai Lake, Ennadai, N.W.T. (0·48–2–3). Ennadai Lake, SW end, 1 mi N of Kazan River (60°45′N, 101°46′W) (0·46–2–3). Angikuni Lake, N.W.T. (62°15′N, 100°00′W) (0·48–1–2) (all this survey). Thelon River system: Whitefish Lake, N.W.T. (62°37′N, 106°45′W) (0·48–1·5–3) (1959, Fish. Res. Bd.!). Prairie Lake, Thelon Game Sanctuary (near 63°43′N, 104°35′W) (0·48 2–3) (1936, C. H. D. Clark!). Dubawnt Lake, N.W.T. (0·50–1·5–3) (1959, Fish. Res. Bd.!). Shultz Lake, N.W.T. (0·50–1·5–3) (1958, Fish. Res. Bd.!). Baker Lake, 13 mi S of Baker Lake settlement (0·50–1–1) (1962, E. W. Smith!). Beverly Lake, SE side, N.W.T. (64°36′N, 100°30′W) (0·50–1–3) (1961, Elizabeth Macpherson!).

Northern Arctic drainage areas. Coppermine River system: Redrock Lake, N.W.T. (65°30′N, 14°24′W) (0·50–1·5–3). Vaillant Lake, N.W.T. (66°12′N, 114°29′W) (0·50–2–3) (both 1959, Fish. Res. Bd.!). Small pool, Coppermine River Bluff, N.W.T. (67°49′N, 115°06′W) (0·46–2–3). Small lake, W side of Coppermine River, 4 mi from river mouth, N.W.T. (0·46–2–3). (both 1957, Fish. Res. Bd!). Anderson River system: Pond on Island, Anderson River, N.W.T. (68°25′N, 128°50′W) (0·50–2–2). Anderson River 35 mi from mouth (0·46–2–3) (both 1958, Fish. Res. Bd!). Husky (Eskimo) Lakes drainage area: Camp lagoon at Husky Lakes, N.W.T. (69°21′N., 133°34′W) (0·48–2–2). Camp stream, Husky Lakes (0·50–2–2). "Drink" Lake, near Camp at Husky Lakes (0·50–2–3) (all 1955, Fish. Res. Bd.!). Victoria Island drainage areas: Lake between Mt. Arrowsmith and Point Williams, Wollaston Peninsula, Victoria I. N.W.T. (0·50–2–3) (1915, Can. Arctic Exped.!).

Mackenzie River system. Liard River drainage area: Pine Lake, Y.T. (60°08′N, 130°55′W) (0·50–2–3) (1965, P. M. Youngman!). Frances Lake, Y.T. (61°25′N, 129°30′W) (1887, G. M. Dawson!). Mackenzie River drainage area: Great Slave Lake, W end, N.W.T. (0·50–2–2) (1919, R. A. Brooks!). Great Slave Lake and vicinity, several localities (0·50–2–3) (1944–46, J. G. Oughton!). Lac La Martre, N.W.T. (63°07′N, 117°48′W) (0·50–2–3) (1959, Fish. Res. Bd.!). Keller Lake, N.W.T. (63°59′N, 121°42′W) (0·48–1·5–3) (1962, Lionel Johnson!). Beaverlodge Lake, N.W.T. (64°42′N, 118°12′W) (0·50–1·5–2) (1959, W. B. Scott!). Fort Norman N.W.T. (0·50–2–3) (1957, Fish. Res. Bd.!). Lac à Jacques, N.W.T. (66°10′N, 127°25′W) (0·46–2–3). Fossil Lake, N.W.T. (66°17′N, 128°53′W) (0·46–1·5–3) (both 1962, E. W. Innes!). Mackenzie River, Aklavik, N.W.T. (0·48–1–3) (1957, Fish. Res. Bd.!).

Distribution: Newfoundland to the vicinity of Hudson Bay, north and northwest in subarctic and arctic Canada to Ungava, southern Victoria Island, the Mackenzie River Delta and the vicinity of Point Barrow, Alaska (NMC specimens). No definite Pleistocene or older occurrences are on record.

Biology and Ecology: Thirty-nine collections of *Lymnaea arctica* were made during this survey. Of these, 6 are from large lakes, 9 are from small lakes, 4 are from permanent ponds, 1 is from a backwater, 2 are from ditches,

14 are from rivers and streams with widths of about 100 feet down to about 4 feet, and 2 are from muskeg pools. Vegetation abundance and substrate characteristics varied widely. At the mouth of the Albany River *L. arctica* occurs in the shallow water of James Bay, but the water there is only faintly saline to the taste. In general, *L. arctica* occupies the same broad spectrum of habitats in the arctic and subarctic that are occupied farther south (or in the lime-rich regions in the subarctic) by *L. elodes* with the exception that *L. arctica* seems to be more tolerant of brackish environments.

The anatomy of *Lymnaea arctica* has been discussed by Hubendick (1951: 100-101, 138) who states that " the most striking morphological feature is. . . the short and pyriform penis sheath and penis " (p. 138).

Topotypes of *Lymnaea arctica* (NMC 19386A-C) and a specimen from the mouth of Goose Creek near Churchill, Man. (NMC 19122A) were examined for radula characteristics with the following results:

Catalogue Number	Shell Length, mm	Radula Formula
19386 A	15·5	$\frac{16}{4\text{-}5}-\frac{3}{3}-\frac{10}{2}-\frac{1}{1}-\frac{10}{2}-\frac{3}{3}-\frac{14}{4\text{-}5}$ (29-1-27)
19386 B	13·9	$\frac{17}{4\text{-}5}-\frac{3}{3}-\frac{10}{2}-\frac{1}{1}-\frac{10}{2}-\frac{3}{3}-\frac{16}{4\text{-}5}$ (30-1-29)
19386 C	12·2	$\frac{18}{4}-\frac{3}{3}-\frac{10}{2}-\frac{1}{1}-\frac{10}{2}-\frac{3}{3}-\frac{17}{4}$ (31-1-30)
19122 A	13·5	$\frac{18}{4\text{-}5}-\frac{2}{3}-\frac{10}{2}-\frac{1}{1}-\frac{10}{2}-\frac{2}{3}-\frac{18}{4\text{-}5}$ (30-1-29)

Egg masses of *Lymnaea arctica* were found 4 times during this survey: on July 7, 1963, in Fort George River, 12 mi E of Fort George, Que.; on July 20, 1966 in Long Lake, Man. (59°24′N, 95°18′W) and in South Henik Lake, N.W.T. (61°30′N, 97°25′W); and on July 22, 1966, in White Stone Lake, Man. (56°27′N, 97°30′W). They were sausage-shaped, transparent,and 10 × 3·5 mm (with 40 embryos), 8 × 2 0 mm (with 14 embryos), 8 × 2·5 mm (with 23 embryos), and 10 × 4 mm (with 12 embryos), respectively. The egg masses were attached to small rocks in each instance.

Remarks: *Lymnaea arctica* is unusually variable even for a lymnaeid. A visual approximation of normal intra-population variability in topotypes of *L. arctica* is shown in Pl. 12, Figs. 4-6. Statistically the intra-population variability of the ratios W/L, Ap L/L, and Ap W/Ap L may be expressed by their coefficients of variability (CV=(S.D. × 100)/Mean) which, in the samples measured in detail (see " Measurements ") varied from 4·5 to 7·1. The

variability of the other population samples appears, on inspection, to be of the same order of magnitude.

It has not been possible in the present study to analyze the variability of all lots of all species for all characters of interest. This would have involved many thousands of measurements and calculations. A few shell characters are here of special interest, however, because (1) they have been used to differentiate taxa within the *Lymnaea arctica* group or are considered otherwise significant, and (2) they are amenable to approximate quantification on inspection. These are as follows:

Relative aperture length: the length of the aperture divided by the length of the shell (Ap L/L, as routinely calculated for lymnaeids)—an approximate mean value for each population sample estimated to the nearest hundredth (0·01).

Relative thickness: estimated by the scale 1, thin; 2, of medium thickness; 3, thick—an approximate mean value estimated to the nearest 0·5.

Crescentric sculpture: the frequency of the crescent-shaped microsculpture estimated by the scale 1, none; 2, present in about half of the specimens; 3, present in all specimens (values estimated to the nearest 0·5).

All population samples available of both *Lymnaea arctica* and the closely-related *L. kennicotti* (compare) were coded for these characters by visual inspection and recorded under " Records ". A series of 3 code numbers has been used, e.g., 0·46-1·5-3, which means ApL/L mean=0·46, shells moderately thin, and all shells with crescentric sculpture.

It was soon apparent that inter-population relative thickness varied independently of geography and that crescentric sculpture occurred in many or all specimens in nearly all populations. Relative aperture length appeared to vary geographically, however, and all lots with mean values below 0·45 were found to be in the western Arctic in the general vicinity of Coronation Gulf. These lots are all similar in general appearance to topotypes of *Lymnaea kennicotti* Baker from Bernard Harbour, N.W.T. and are considered to be that species. *L. kennicotti* is discussed below.

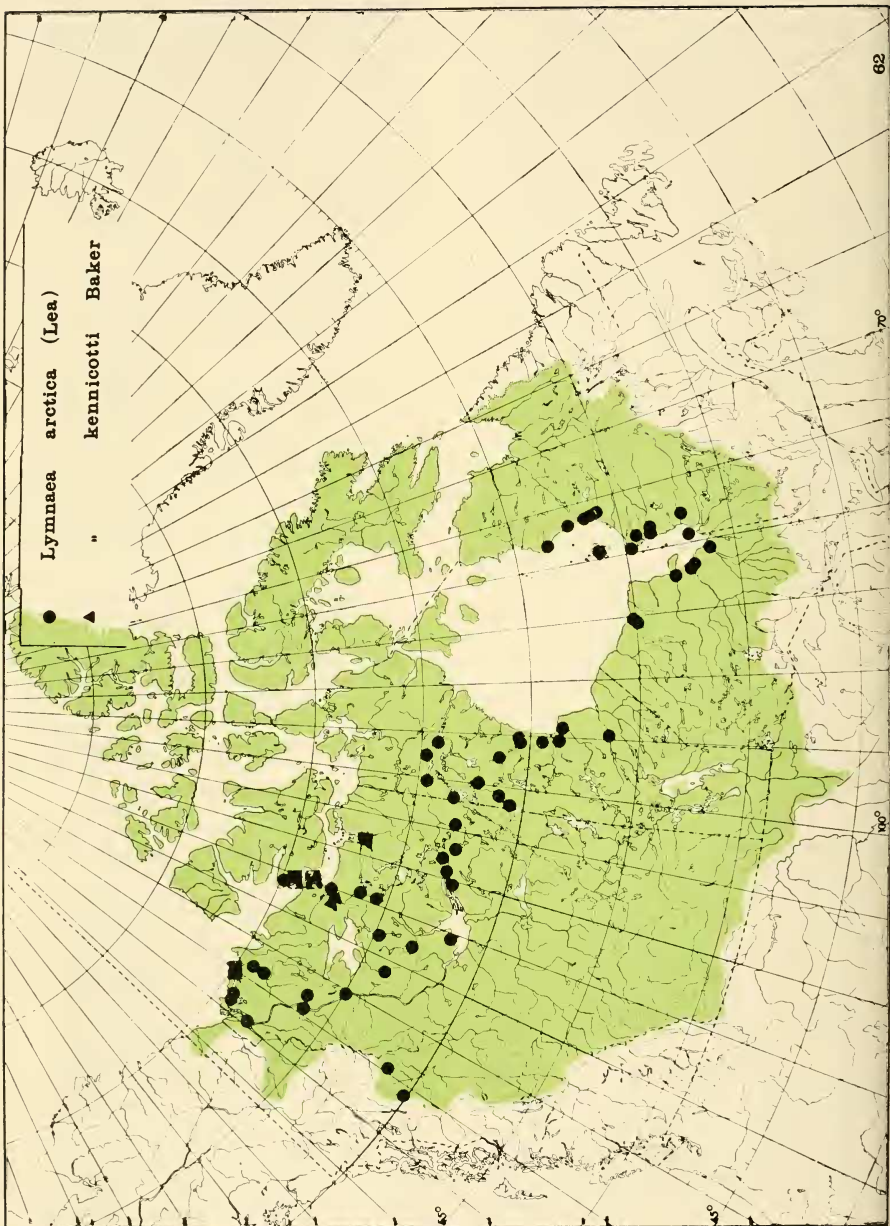
High values of Ap L/L (above 0·55) are concentrated in the vicinity of Hudson Bay and James Bay and lots with intermediate values (0·45-0·55) are generally spread over the whole range of *L. arctica*. Although a diffuse cline exists between low values in the east and intermediate values in the north-west, so many exceptions to the trend occur that no taxonomic distinction between them, other than the separation of *Lymnaea kennicotti*, appears justified.

Lymnaea kennicotti (Baker)
Plate 23, Fig. 5; Map 62.

Stagnicola kennicotti Baker, 1933: New species of Lymnaeidae from British America. *J. Wash. Acad. Sci.*, *23*(11): 522, fig. 1, lower row, 3 figs. at left. Type locality: " Creek at Barnard Harbor [Bernard Harbour, 68°45′N, 114°45′W], near Coronation Gulf, Mackenzie District [Northwest Territories], Canada."

Diagnosis: Shell medium sized, solid, with rounded whorls, elongate spire, and relatively small, ovate aperture.

Description: Shell up to nearly $\frac{7}{8}$ inch long, pale brown, relatively solid, and with a rather long spire and a roundly ovate aperture which is about 40% as long as the shell. Nuclear whorls satiny, about $1\frac{1}{2}$ to 2 in number, and forming a high, dome-shaped apex. Spire long and acute. Whorls about $6\frac{1}{2}$ to 7 and rounded. Outer lip thin, convex, and without an internal varix. Inner lip flattened, rather wide, reflected over the umbilical region, and gently curved or angular (in some specimens)


Lymnaea arctica (Lea)
" kennicotti Baker

at the junction of the columella and the part appressed to the preceding whorl. Umbilicus visible only as a small, narrow chink. Sculpture consisting of irregular collabral lines, numerous low spiral ridges, and spiral rows of tiny crescents between the ridges. As in the several other species with crescentric sculpture the ends of the crescents are directed away from the aperture. Crescents are unusually obvious on this species, even under only 12x magnification. The periostracum is closely adherent and of a pale horn colour.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Creek, Bernard Harbour, N.W.T. (topotypes of *L. kennicotti*).					
Length (L), mm	30	13·8 —20·2	16·46	—	—
W/L	30	0·45 — 0·52	0·482	0·004	0·022
Ap L/L	30	0·34 — 0·45	0·413	0·004	0·022
Ap W/Ap L	30	0·48 — 0·69	0·519	0·006	0·032
Whorls	30	6·0 — 7·0	6·55	—	—
Creek, " Nariat," Wollaston Peninsula, Victoria I., N.W.T.					
Length (L), mm	4	15·7 —21·2	17·72	—	—
W/L	4	0·48 — 0·50	0·490	—	—
Ap L/L	4	0·44 — 0·45	0·444	—	—
Ap W/Ap L	4	0·49 — 0·51	0·505	—	—
Whorls	4	6·6 — 7·0	6·82	—	—

Records:

Code numbers refer to morphological characters. See "Remarks" under the preceeding species, *Lymnaea arctica*.

Northern Arctic drainage areas. Small unnamed lake West of Bathurst Inlet, N.W.T. (66°32′N 107°42′W) (0·40–2–3) (1962, W. Blake Jr.), Creek at Bernard Harbour, N.W.T. (68°45′N, 114°45′W) (topotypes of *L. kennicotti*) (0·41–2–3). Creeks and lake at Bernard Harbour, N.W.T. (0·41–2–3) (both July 5, 1916, Can. Arctic Exped.!). "Creek at Nariat (between Cape Baring and Pullen Point) Wollaston Id." [Wollaston Peninsula, Victoria Island, near 69°00′N, 116°00′W, N.W.T.] (0·44–2·5–3) (Aug. 31, 1915, Can. Arctic Exped.!). Spring run-off pool, Coppermine River bluff (67°49′N, 115°06′W) (juveniles) (1957, Fish. Res. Bd.!). Dismal Lake, N.W.T. (67°13′N, 116°38′W) (0·44–2–3) (1959, Fish. Res. Bd.!). Nicholson Island, Liverpool Bay, N.W.T. (69°45′N, 130°00′W) (0·44–2–3) (1955, Fish. Res. Bd.!).

Distribution: The mainland arctic coast of Canada and vicinity from near Bathurst Inlet, N.W.T. west to Liverpool Bay, N.W.T.; also southern Victoria Island, N.W.T.

Biology and Ecology: From the records above it appears that *Lymnaea kennicotti*, like many other lymnaeids, occupies a wide range of habitats. It has been found in large lakes, in small lakes, in pools, and in creeks.

Nothing has been published concerning the anatomy or radula of this species. Specimens of *Lymnaea kenni-*

PLATE 23. *Lymnaea* (III)

FIG. 1. *Lymnaea stagnalis sanctaemariae*, Dog Lake, Ontario (NMC 2151, 53 mm), ... p 305.

FIG. 2. *Lymnaea atkaensis*, Near Cape Parry, Northwest Territories (NMC 19822, 35 mm), ... p 308.

FIG. 3. *Lymnaea catascopium preblei*, Limestone Lake, Manitoba (NMC 37378, 38 mm), ... p 349.

FIG. 4. *Lymnaea catascopium nasoni*, Lake of the Woods, Kenora, Ontario (NMC 25047, 9·1 mm), ... p 347.

FIG. 5. *Lymnaea kennicotti*, Creek at Bernard Harbour, N.W.T. (NMC 4016A, 18 mm), ... p 323.

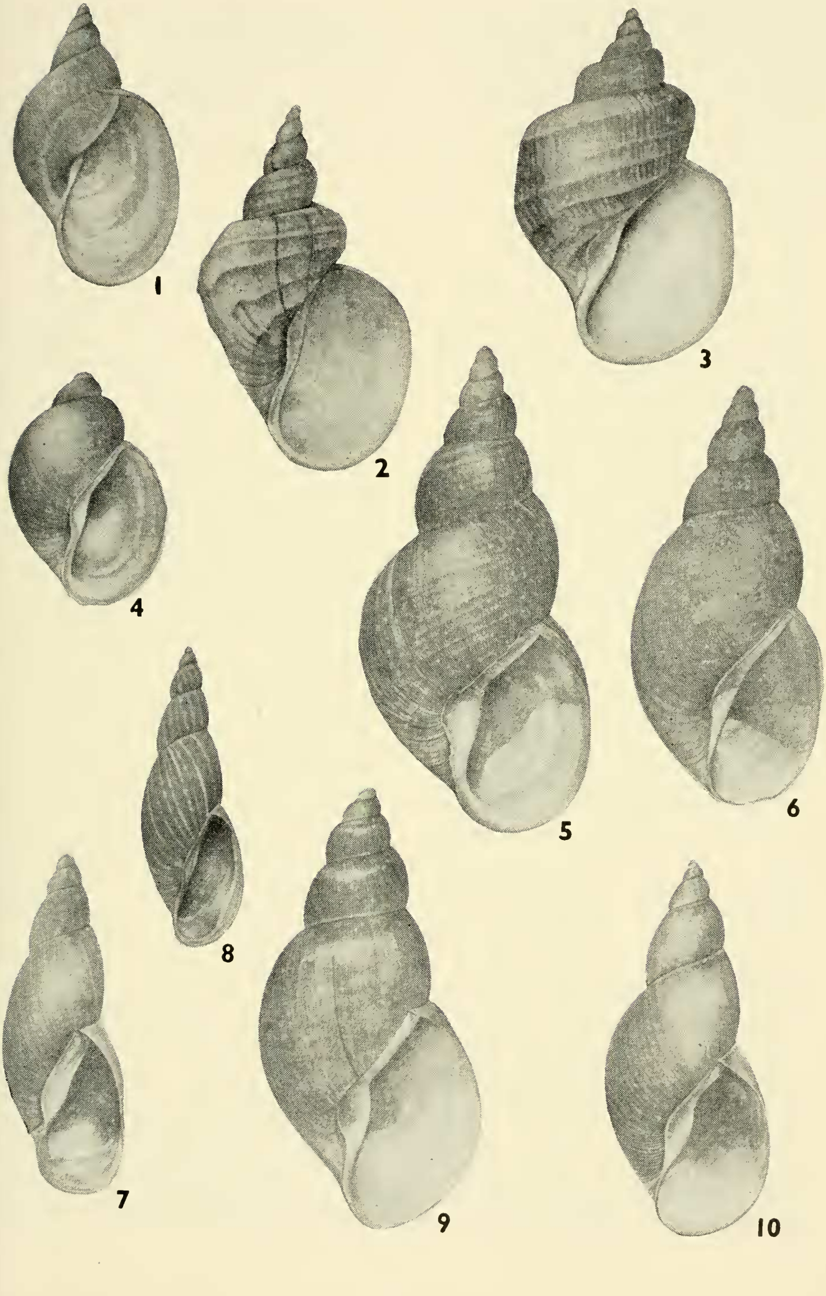
FIG. 6. *Lymnaea proxima*, Banff, Alberta (NMC 45532, 16 mm),. . . . . p 355.

FIG. 7. *Lymnaea reflexa*, Midway Lake, near La Ronge, Saskatchewan (NMC 38044, 26 mm), ... p 358.

FIG. 8. *Lymnaea reflexa*, near Star Lake, Whiteshell Provincial Park, Manitoba (NMC 23925, 23 mm), ... p 358.

FIG. 9. *Lymnaea elodes* (*ungava* morph), False River pond, near Ungava Bay, Quebec (NMC 29027, 16 mm), ... p 355.

FIG. 10. *Lymnaea elodes*, near Lindbrook, Alberta (NMC 28141, 28 mm), ... p 351.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cotti from Dismal Lake, N.W.T. contained dried soft parts and were examined for radula characteristics with the following results:

Catalogue Number	Shell Length, mm	Radula Formula
30682 A	12·5	$\frac{19}{4}-\frac{4}{3}-\frac{10}{2}-\frac{1}{1}-\frac{10}{2}-\frac{4}{3}-\frac{18}{4}$ (33–1–32)
30682 B	13·6	$\frac{20}{4}-\frac{3}{3}-\frac{9}{2}-\frac{1}{1}-\frac{9}{2}-\frac{3}{3}-\frac{19}{4}$ (32–1-31)
30682 C	11·9	$\frac{17}{4\text{–}5}-\frac{3}{3}-\frac{9}{2}-\frac{1}{1}-\frac{9}{2}-\frac{3}{3}-\frac{17}{4\text{–}5}$ (29–1–29)

Remarks: *Lymnaea kennicotti* is more closely related to *L. arctica* than to any other species. Points of difference in shell characters are chiefly the much more elongate form and smaller, rounder aperture in *L. kennicotti* (compare measurements). See " Remarks " under *L. arctica*.

Since the populations of *L. kennicotti* all occur in a given region and since some populations of *L. arctica* occur in the same region (e.g., on Wollaston Peninsula, Victoria Island) without intergrades, it is believed that *L. kennicotti* is a separate species and not a subspecies of *L. arctica*.

The distribution of *Lymnaea kennicotti* is characteristic of a glacial relict species, being similar to *L. atkaensis* and *Anodonta beringiana* in this respect.

Lymnaea catascopium catascopium Say
Plate 12, Figs. 7, 8; Map 63.

Lymnaea catascopium Say, 1817: *Nicholson's Encyclopedia*. 1st. Amer. ed., *2*, pl. 2: 3 (Binney reprint, 1858: 45). Type locality: " Inhabits the Delaware River and many other waters of the United States, in considerable numbers, and may be found plentifully, during the recess of the tide, about the small streams through which the marshy ground is drained, in company with several other shells."

Lymneus emarginatus Say, 1821: *J. Acad. natr. Sci. Philad.*, *2*: 170 (Binney reprint, 1858: 67). Type locality: " Lakes of Maine."

Lymnaea apicina Lea, 1839: *Trans. Amer. phil. Soc.*, *6*: 102, pl. 23: 94. Type locality: " Wahlamat [Willamette River], near its junction with the Columbia River."

Limnea serrata Haldeman, 1842: *Monograph of the freshwater univalve Mollusca of the United States*. Genus *Limnea*, p 12, pl. 2: 6–8. Type locality: " North-west Territory."

Limnaeus ontariensis " Muhlfeld " Küster, 1862: (*in*) *Chemnitz Conchylien Cabinet*. *Ed*. 2, Abt. b, p 45 (as Var. A under " *Lymnaeus* " *emarginatus* Say). Type locality : " in Ontario—See."

Limnaea mighelsi Binney, 1865: Land and Fresh Water Shells of North America, *2*: 31. New name for *Limnaea ampla* Mighels 1843, non Hartmann, 1842. Type locality: " Second Eagle Lake, Aroostook Co., Maine."

Limnaea binneyi Tryon, 1865: *Amer. J. Conchol.*, *1*: 229, pl. 23: 3. Type locality: " Hell Gate River, Oregon."

Limnaea canadensis Sowerby, 1872: *Conchologica Iconica*, *18*, Limnaea, species 45, pl. 7: 45a, a. Type locality: " Canada."

Lymnaea pilsbryana Walker, 1908: *Nautilus*, *22*(1): 4–5, pl. 1: 2, 8–11. Type locality: " Washington Harbor, Isle Royale, Lake Superior, Michigan."

Lymnaea emarginata wisconsinensis F. C. Baker, 1910: *Nautilus*, *24*(4): 58; Baker, 1911: *Lymnaeidae of North and Middle America*. p 425, pl. 44: 10–18. Type locality: " East shore Tomahawk Lake, Oneida Co., Wis."

Stagnicola walkeriana F. C. Baker, 1926: *Nautilus*, *39*(4): 119–121; Baker, 1928: *Fresh Water Mollusca of Wisconsin*. pt. 1, p 247–280, pl. 17: 1–11. Type locality: " Madeline Island, near Bayfield, Bayfield Co., Wisconsin."

Stagnicola emarginata vilasensis F. C. Baker, 1927: *Nautilus*, *40*(3): 82–84; Baker, 1928: op. cit., *1*: 243–245, pl. 16: 21–26. Type locality: " Big Muskallonge Lake, Vilas Co., Wisconsin."

Stagnicola catascopium kempi F. C. Baker and A. R. Cahn, 1931: *Nat. Mus. Can. Bull.*, 67: 53–54, pl. 2: lower 2 rows. Type locality: "Bamaji Lake outlet on rocks and in rapids [northern Ontario]."

Stagnicola elrodi F. C. Baker & J. Henderson, 1933: *Nautilus*, *47*(1): 30–32. Type locality: "West shore Flathead Lake, 13½ miles north of Polson, Montana."

Diagnosis: Shells relatively short, variable, small-medium to large, with aperture ovate and as long as or longer than the spire, and nearly smooth to heavily sculptured.

Description: Shells of adult specimens from about ½ to 1¼ inches high, exhibiting unusually high intra- and inter-population variation, relatively short and ovate, greyish-brown to brown, with or without a columella plait, an open umbilicus, and strong surface sculpturing. Nuclear whorls 1½, wide, low, and chestnut coloured. Whorls about 5, rounded to subglobose, shouldered in some specimens, and forming a pyramidal to flattened spire. Sutures well impressed to deeply incised. Body whorl dominant and, in many specimens, irregularly rounded. Aperture ovate to subquadrate, very large, expanded and flaring in some specimens, and more than half the height of the shell in nearly all specimens. Outer lip thin but in many specimens thickened within by a varix which may be edged with brown. Inner lip with a broad callus which is partially or completely reflected over the umbilicus in most specimens and smooth or with a columella plait variously developed. Spiral sculpture varying between specimens (and in some cases on different parts of the body whorl of the same specimen) from nearly absent to strong and composed of spiral lines, ridges, or flat bands. Collabral sculpture consisting of lines of growth of varying prominence. In some specimens widely spaced, white collabral bands are present corresponding to previously formed apertural varices.

Measurements*:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Lake 18 mi E of Chin Coulée, Alta.					
Length (L), mm	30	18·5 —25·1	20·45	—	—
W/L	30	0·59— 0·76	0·668	0·009	0·048
Ap L/L	30	0·50— 0·64	0·550	0·007	0·038
Ap W/Ap L	30	0·46— 0·65	0·540	0·006	0·035
Whorls	20	4·0 — 5·5	4·60	—	—
North shore, Clear Lake, Man.					
Length (L), mm	25	17·2— 29·3	22·13	—	—
W/L	25	0·54— 0·68	0·619	0·006	0·028
Ap L/L	25	0·48— 0·63	0·546	0·008	0·042
Ap W/Ap L	25	0·47— 0·60	0·525	0·006	0·030
Whorls	18	5·3 — 6·3	5·83	—	—

* See Charts 15 to 25, and populations 1–5, 7–15 for more extensive measurements.

Feature	N	Range	Mean	$S.E._M$	S.D.
Nagagamisis Lake, 20 mi N of Hornepayne, Ont.					
Length (L), mm	11	19·9 —32·8	26·44	—	—
W/L	11	0·60— 0·75	0·696	0·012	0·039
Ap L/L	11	0·56— 0·68	0·624	0·009	0·031
Ap W/Ap L	11	0·50— 0·60	0·540	0·009	0·029
Whorls	10	5·2 — 6·4	5·69	—	—

Records:

Eastern Hudson Bay and Eastern James Bay drainage areas. Lower Char Lake, near Richmond Gulf, Que. Burton Lake, N side near middle, 33 mi SSW of Poste de la Baleine (Great Whale River), Que. Waswanipi River, 22 mi NE of Demaraisville, Que. (all this survey).

Moose River system. Abitibi River, 12 mi N of Iroquois Falls, Ont. Shipsands Island, mouth of Moose River, Ont. (both 1933, H. G. Richards!).

Albany River system. Lake Nipigon, Ont. (1884, J. Macoun!). Nagagamisis Lake, 20 mi N of Hornepayne, Ont. Nagagami River, 40 mi W of Hearst, Ont. Outlet of Lake St. Joseph, Rat Rapids, Ont. (all this survey). Bamaji Lake at outlet, Ont. (cotypes of *S. c. kempi* F. C. Baker). Pashkokogan River, Ont. (both 1929, A. R. Cahn!). Yellow Creek, near Fort Albany, Ont. (this survey).

Attawapiskat River system. Crow River and Ozhiski Lake, Ont. (both 1904, W. McInnes!). Monument Channel at portage to Attawapiskat River, 20 mi W of Attawapiskat, Ont. Monument Channel 12 mi W of Attawapiskat. Attawapiskat River 6 mi W of Attawapiskat. South shore of Attawapiskat River near mouth (all this survey).

Winisk River system. Wapitotem River, Mistassin Lake, and "Dashka Rapids", Winisk River (1903 and 1904, W. McInnes!). Small brook entering Winisk River 5 mi E of Winisk, Ont. Shore of Hudson Bay near N side of Winisk River mouth (in drift) (both this survey).

Severn River system. Big Trout Lake, Ont. (1905, W. McInnes!). Big Trout Lake near Post Island. Severn Lake, north end, Ont. (54°05′N, 90°42′W) (both this survey).

Winnipeg River system. Basswood River Rapids, Ontario-Minnesota boundary (1929, A. R. Cahn!).

Red River system. Lower Red Lake, 1 mi S of outlet into Red Lake River, Minn. (this survey).

Saskatchewan River system. Waterton Lake, Alta. (1883, J. B. Tyrrell!). Lake 18 mi E of Chin Coulée, Alta. (1883, T. C. Weston!). Creek 4 mi E of Pense, Sask. Moose Jaw Creek, 12 mi SE of Moose Jaw, Sask. Clear Lake, Wasagaming, Man. (all this survey). North shore of Clear Lake (1935, W. E. Swales!, also this survey). Rocky Lake, 29 mi N of The Pas, Man. (this survey). Cormorant Lake, Man. (1906, W. McInnes!).

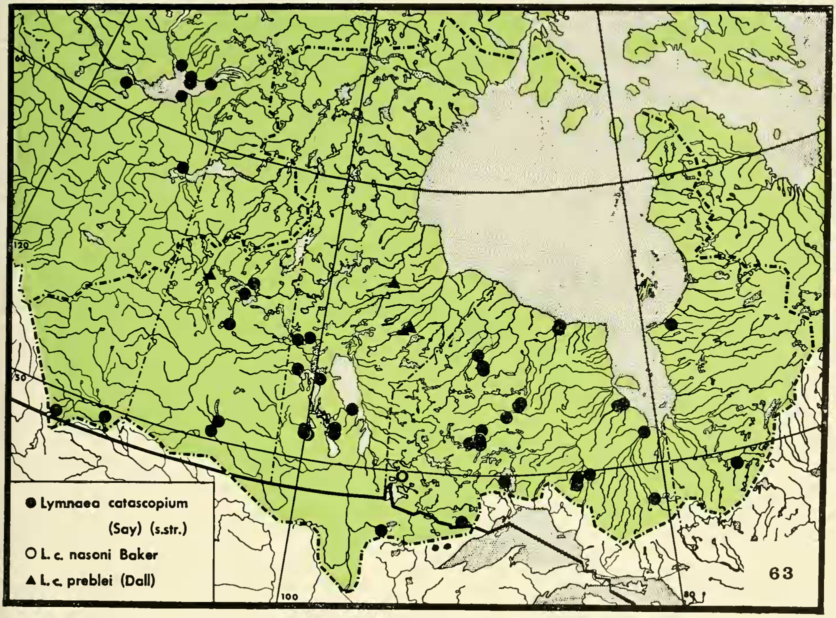
Lake Manitoba—Lake Winnipegosis drainage areas. Lake Manitoba: 7 mi W of Ashern, 15 mi W of Benhorn, and 7 mi N of Moosehorn. Denbeigh Point, NE corner of Lake Winnipegosis, Man. (all 1964, M. Ouellet!). NW corner of Lake Winnipegosis, 13 mi N of mouth of Red Deer River, Man. (this survey).

Nelson River system. Lake Winnipeg, entrance to Kinwow Bay, Man. (52°00′N, 97°33′W) (1890, Lambe!) Cormorant Lake (1906, W. McInnes!).

Churchill River system. Montreal Lake, south end, 16 mi N of Waskesiu Lake, Sask. Rocky islet ½ mi offshore Waden Bay, Lac la Ronge, Sask. Otter Rapids, Churchill River, 54 mi N of La Ronge, Sask. (all this survey).

Mackenzie River system. Peace River just below Point Providence, Alta. (58°57′N, 112°03′W) (1921, G. S. Horne and E. J. Whittaker!). Great Slave Lake and vicinity, numerous collections (1944–46, J. G. Oughton!). Lake Kakisa, N.W.T. (61°03′N, 117°10′W) (1921, E. J. Whittaker!). Fawn Lake, Horn River, N.W.T. (62°12′N, 117°30′W). Big Island, head of Mackenzie River, N.W.T. (both E. J. Whittaker, 1924: 8–12).

Distribution: Gulf of St. Lawrence to Delaware River and west: in the Upper Mississippi River and Great Lakes-



St. Lawrence River systems, in the Rocky Mountain region (south to about 40°N) and in Washington and British Columbia. The northern limit of *Lymnaea catascopium* extends east of Hudson Bay and James Bay north at least to Richmond Gulf (56°N), west along the southern edge of Hudson Bay, and northwest to the vicinity of Great Slave Lake (See Map 63, and " Records "). This species has no known fossil record.

Biology and Ecology: Of the 27 collections of *Lymnaea catascopium* made during this survey, 12 are from large lakes, 1 from a small lake, 3 from permanent ponds, 3 from backwater areas of streams, 5 from rivers over 100 feet wide, 1 from a river 75 feet wide, 1 from a river 40 feet wide, and 1 from a brook only 3 feet wide but within 100 yards of its entrance to a large river (the Winisk River). Aquatic vegetation was present (sparse to thick) at all localities and bottom sediments were of all types except clay, with rocks being a prominent feature at 10 of the stations. In stream habitats the currents were of all velocities up to rapid (i.e., with riffles).

Mozley (1938: 103) gives exposed shores of large lakes as the usual habitat of both " *Lymnaea* (*Stagnicola*) *catascopium* " and " *L.* (*S.*) *emarginata* ". Baker (1911: 387) says " plentiful in large bodies of water such as lakes, rivers, and bays " for *L. catascopium*. For *L.* " *emarginata* " (loc. cit., p 414) he gives rocks in large lakes as a typical habitat, and also mentioned finding a relationship between large shells (" variety *mighelsi* ") with large bodies of water and of smaller shells with smaller water bodies.

The anatomy of this species has been discussed by Baker (1911: 384-385, etc., 1928a: 237-8, etc.). A much more complete anatomical study has recently been published by Walter (1969). The radula is quoted by Baker as $\frac{22}{5-7} - \frac{4}{3-4} - \frac{9}{2} - \frac{1}{1} - \frac{9}{2} - \frac{4}{3-4} - \frac{22}{5-7}$ (35-1-35) for *Lymnaea catascopium* and $\frac{23}{4-6} - \frac{2}{3} - \frac{10}{2} - \frac{1}{1} - \frac{10}{2} - \frac{2}{3} - \frac{23}{4-6}$ (35-1-35) for *L. emarginata*, although some variation is also noted.

Specimens collected during this survey agree in general with Baker's formulae. One specimen 11·8 mm long from Burton Lake in northern Quebec had the formula $\frac{21}{4-5} - \frac{2}{3} - \frac{8}{2} - \frac{1}{1} - \frac{8}{2} - \frac{2}{3} - \frac{20}{4-5}$ (31-1-30). Another, 16·9 mm long from Nagagami River, 40 mi W of Hearst, Ont., had the formula $\frac{20}{4-6} - \frac{3}{3} - \frac{9}{2} - \frac{1}{1} - \frac{9}{2} - \frac{3}{3} - \frac{19}{4-6}$ (31-1-31).

Remarks: According to Baker (1911: 1928a: 7, etc.), principally on the basis of shell characters, the relatively wide and heavily sculptured stagnicoliform lymnaeids characteristic of large water bodies are in 2 related species groups. These groups are designated as the "*Stagnicola catascopium* group" and the "*S. emarginata* group" (Baker, 1911) or combined under a single heading (the "*S. emarginata* group") (Baker, 1928a) but still retaining sub-group relationships. Members of the "*S. catascopium* group" exhibit a narrower shell, a narrow inner lip which is closely appressed to the umbilical region, and an umbilicus which, if present at all, is small and narrow. Members of the "*S. emarginata* group" have a relatively wider shell, a wide and broadly reflected inner lip, and a large and conscpicuous umbilicus. The various species and subspecies within each group are also distinguished by shell characters and no significantly different anatomical characters have been noted. More recently, Hubendick (1951: 132) has stated that there are no features of the copulatory organs or of the radula which distinguish *S. catascopium* from *S. emarginata*. Both "species" are also anatomically similar but, since their ecology is different, they were retained as distinct. Walter (pers. comm.), on the basis of extensive anatomical studies, has also affirmed that their anatomical features are identical.

In order to identify the collections available it was necessary to evaluate the numerous relevant species and subspecies in the *Lymnaea catascopium*-*L. emarginata* groups. Population samples (Table 7) from localities generally spread throughout the study area were measured and classed for all shell characters which have been used to define taxa within these groups. The results were analyzed statistically and are shown on Charts 15 to 26.

Characters measured (in mm) and numerically classed are abbreviated and defined as shown below. (Numerically classed characters were often assigned intermediate values, as 1·7, 2·4 etc.)

L	Length (or height), the maximum distance from the apex to the base of the aperture measured along the shell axis.
W/L	Maximum width (measured perpendicular to the length) divided by length.
Ap L/L	Maximum aperture length (measured parallel to the length) divided by the shell length.
Ap W/Ap L	Aperture width (measured perpendicular to the length) divided by aperture length.

CHART 15. *Lymnaea catascopium* populations. For explanation see p 332. Symbols are defined in caption for Chart 1.

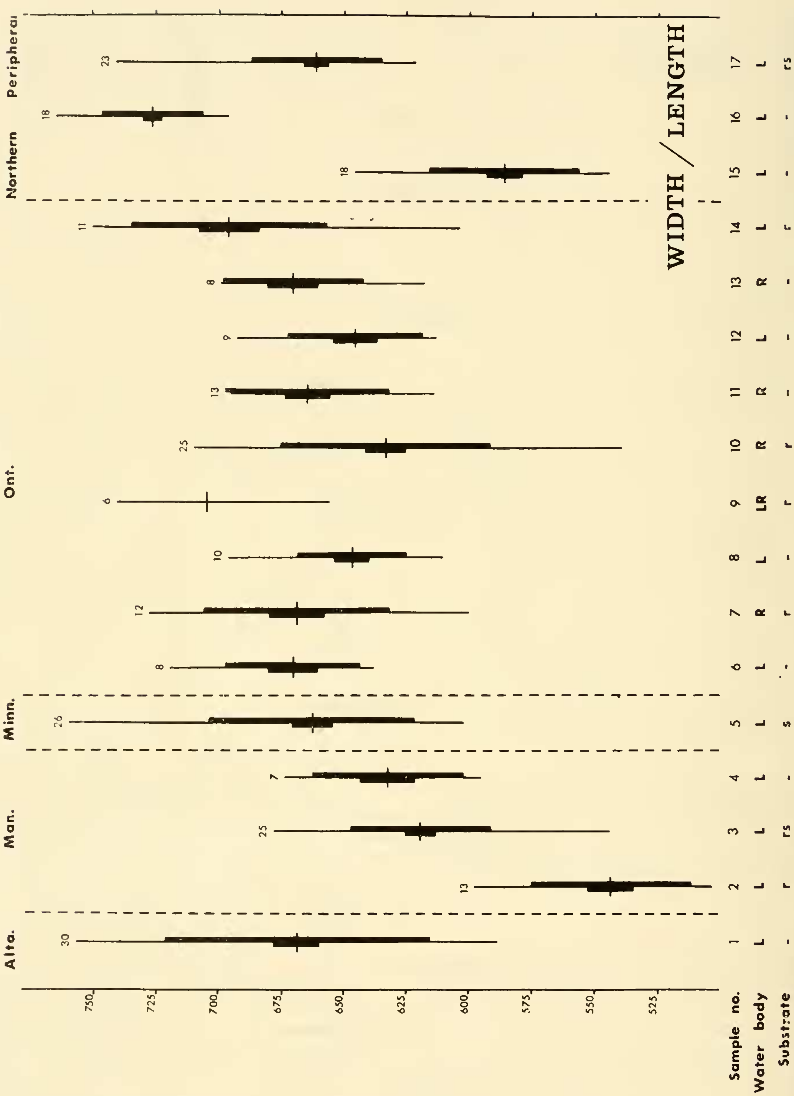


CHART 16. *Lymnaea catascopium* populations. For explanation see p 332. Symbols are defined in caption for Chart 1.

CHART 17. *Lymnaea catascopium* populations. For explanation see p 332. Symbols are defined in caption for Chart 1.

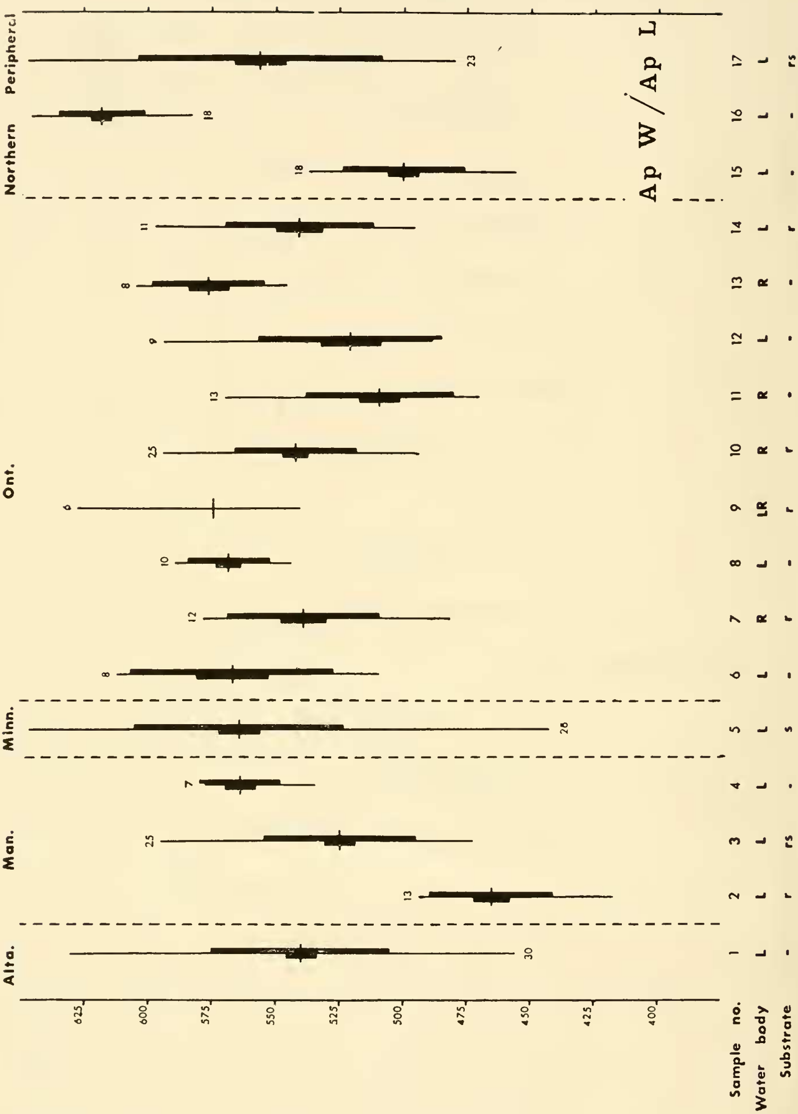


CHART 18. *Lymnaea catascopium* populations. For explanation see p 332. Symbols are defined in caption for Chart 1.

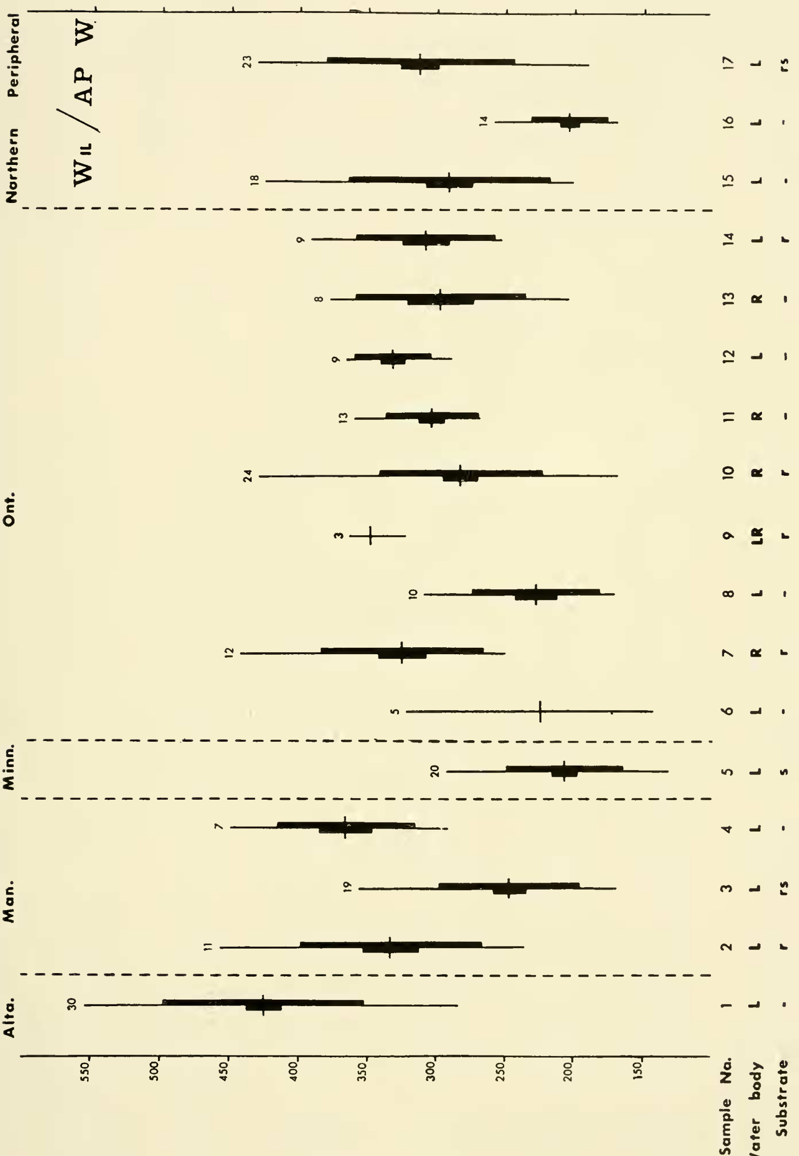


CHART 19. *Lymnaea catascopium* populations. For explanation see p 345. Symbols are defined in caption for Chart 1.

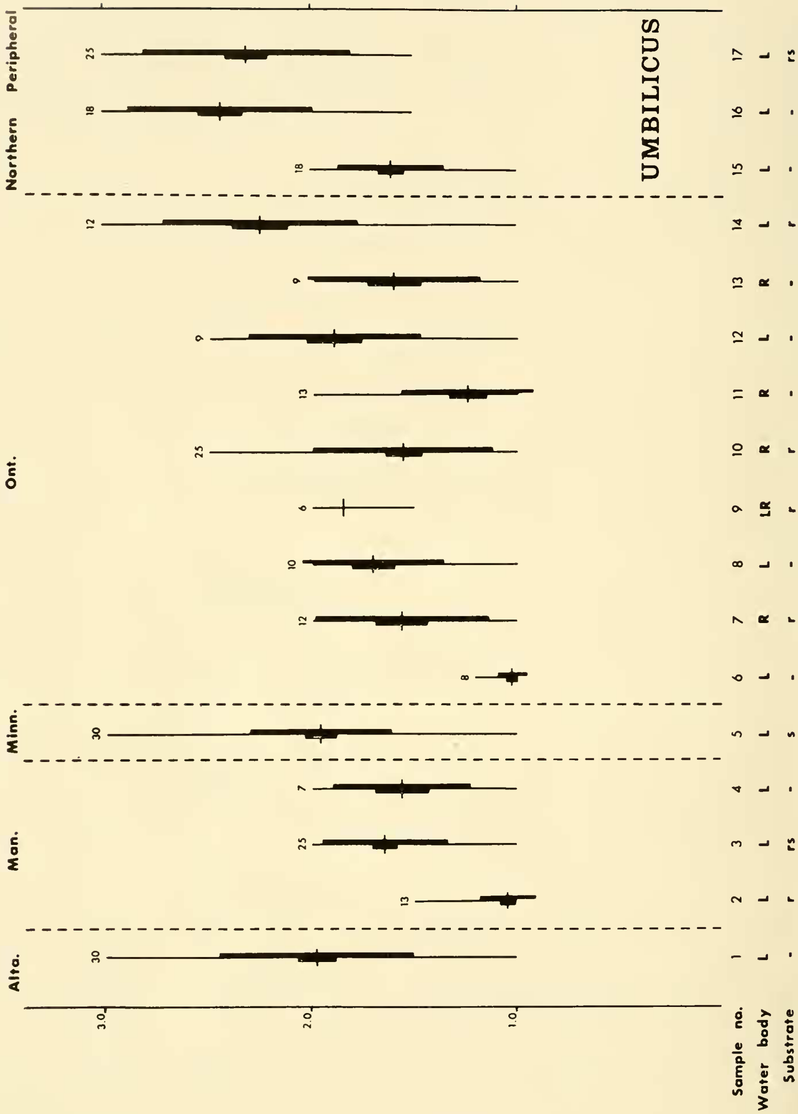


CHART 20. *Lymnaea catascopium* populations. For explanation see p 345. Symbols are defined in caption for Chart 1.

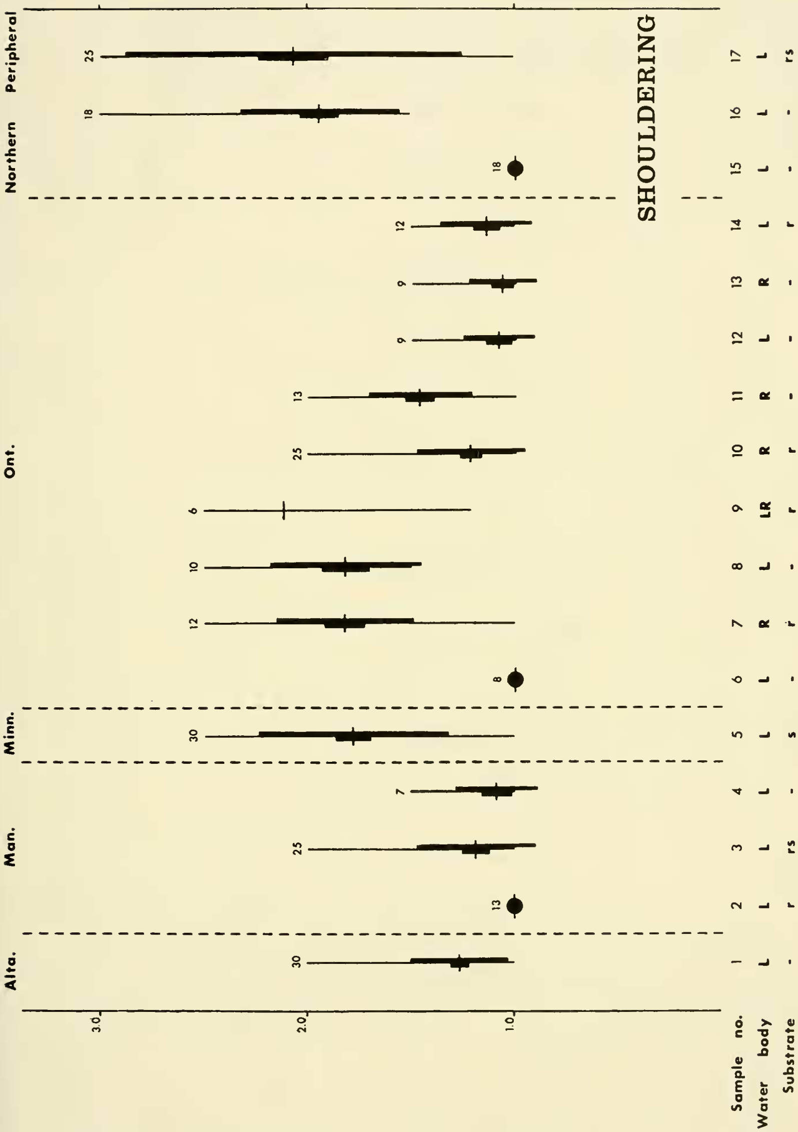


CHART 21. *Lymnaea catascopium* populations. For explanation see p 345. Symbols are defined in caption for Chart 1.

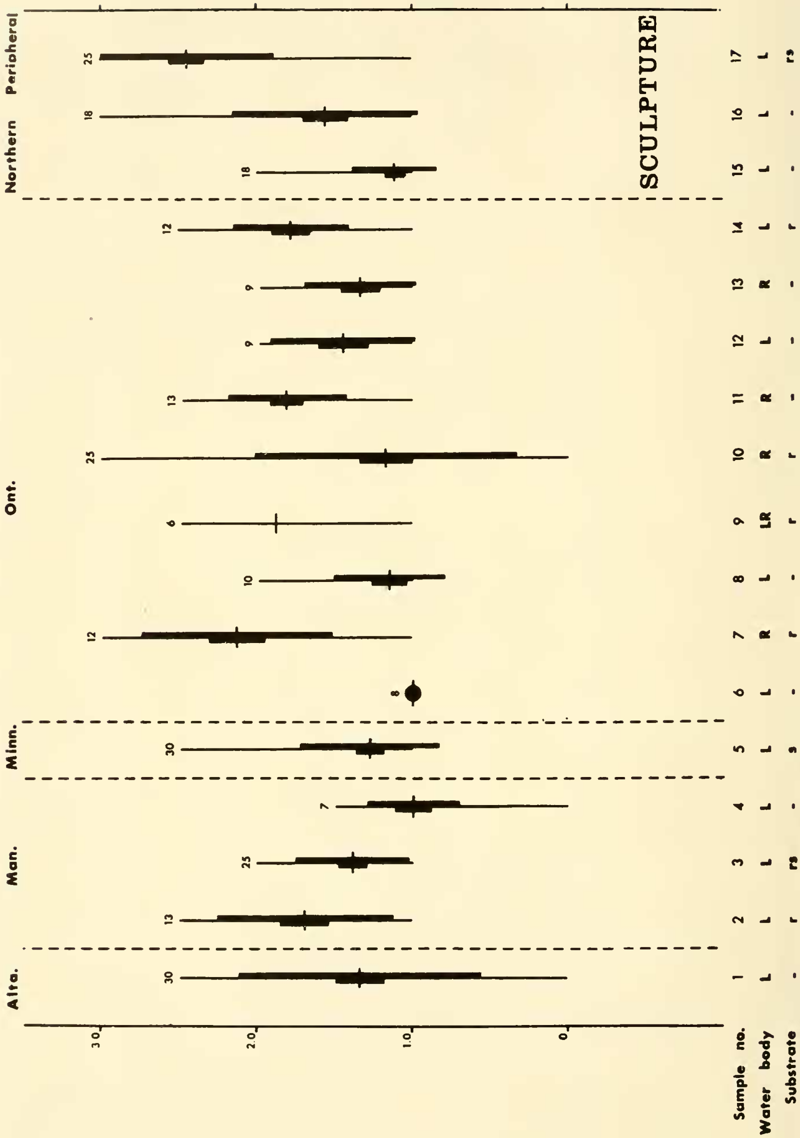


CHART 22. *Lymnaea catascopium* populations. For explanation see p 345. Symbols are defined in caption for Chart 1.

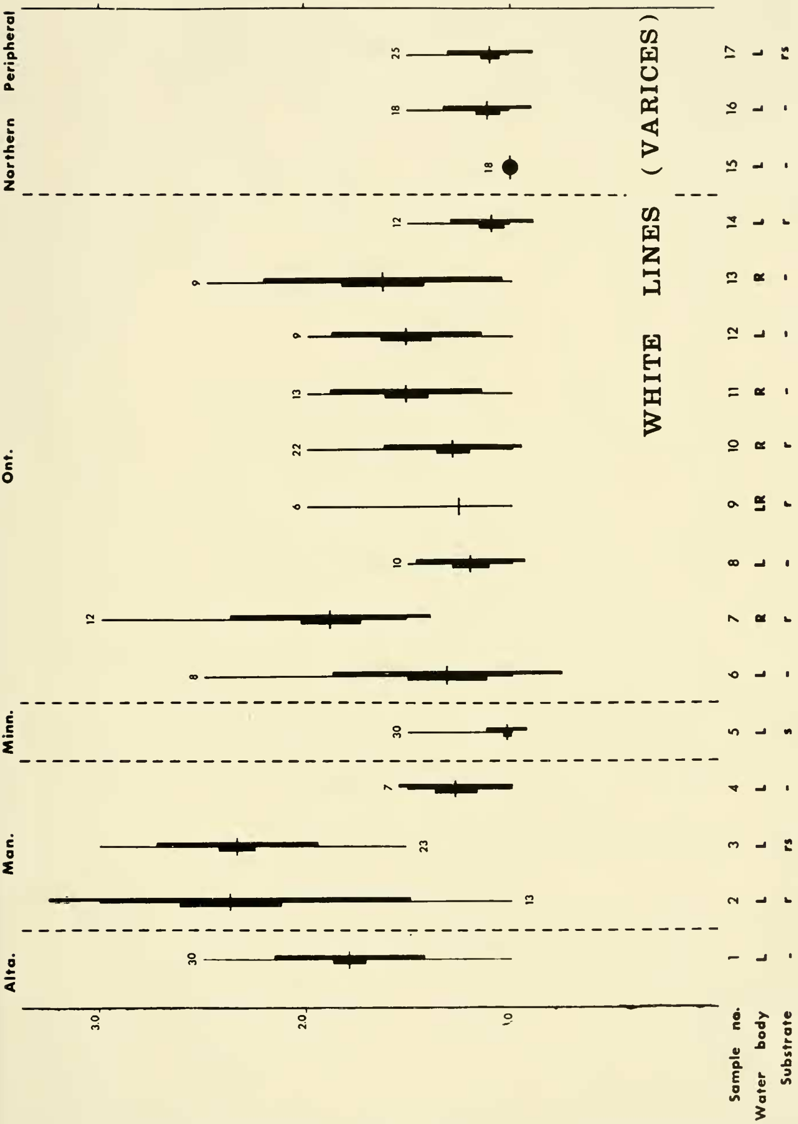


CHART 23. *Lymnaea catascopium* populations. For explanation see p 345. Symbols are defined in caption for Chart 1.

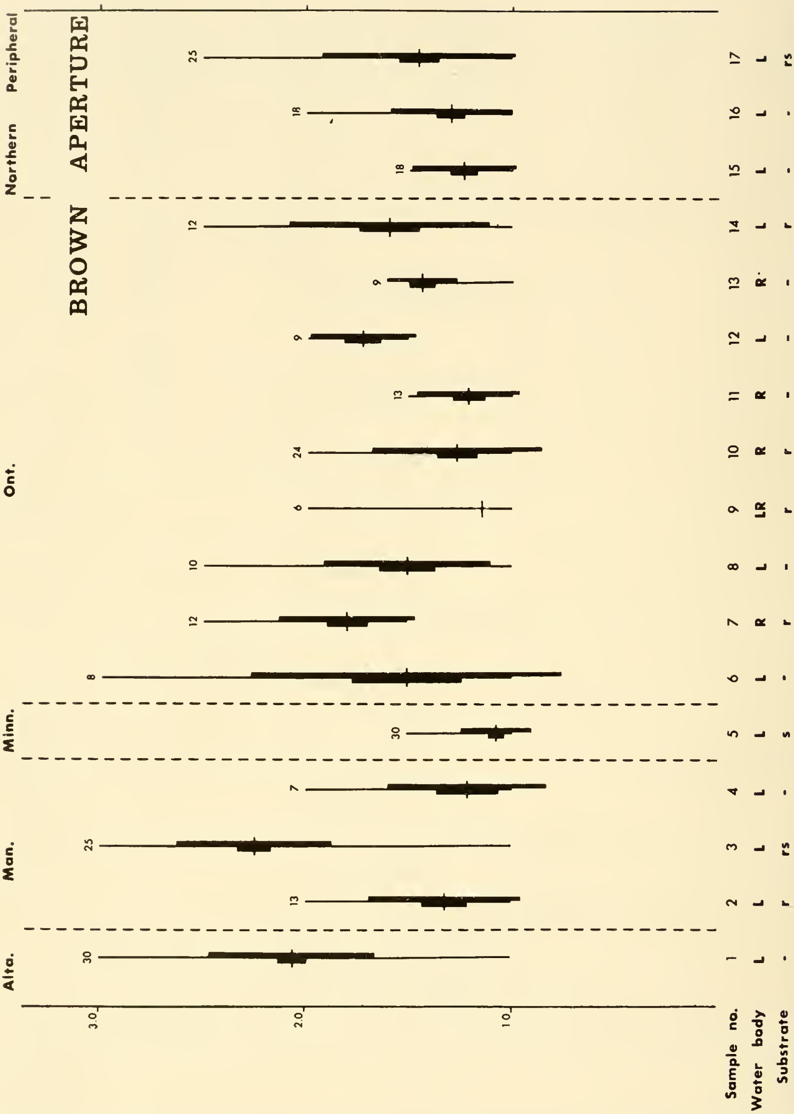


CHART 24. *Lymnaea catascopium* populations. For explanation see p 345. Symbols are defined in caption for Chart 1.

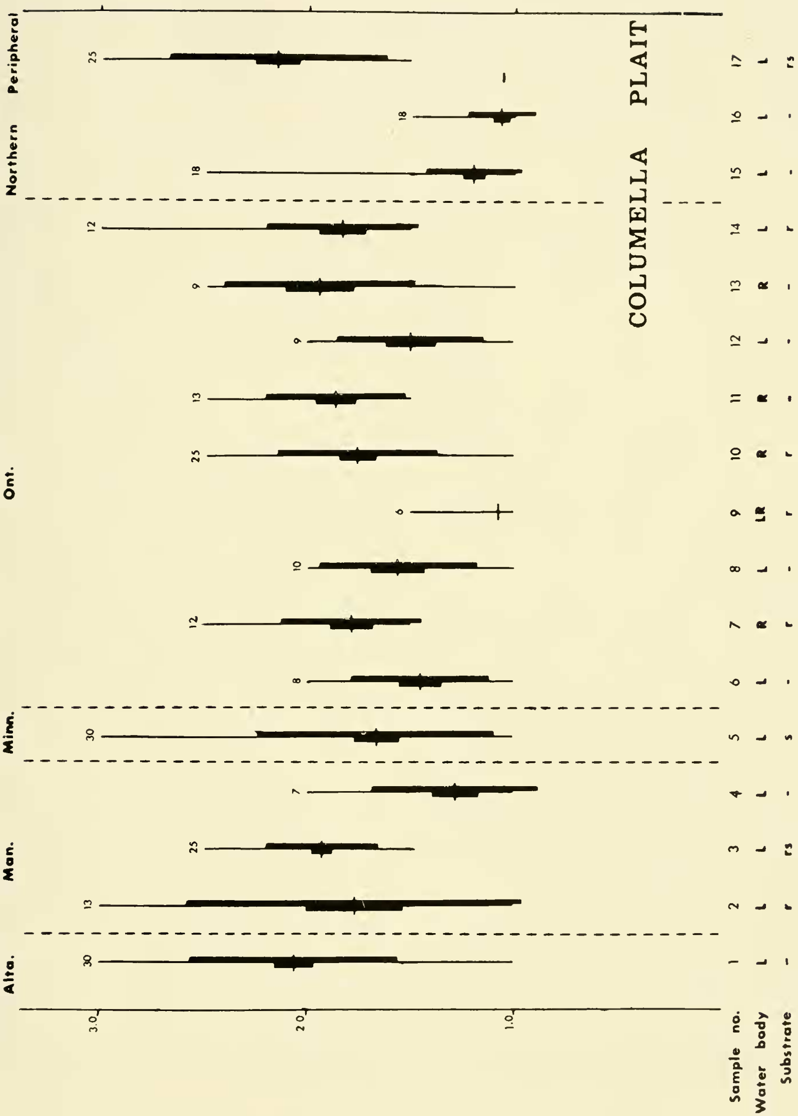


CHART 25. *Lymnaea catascopium* populations. For explanation see p 345. Symbols are defined in caption for Chart 1.

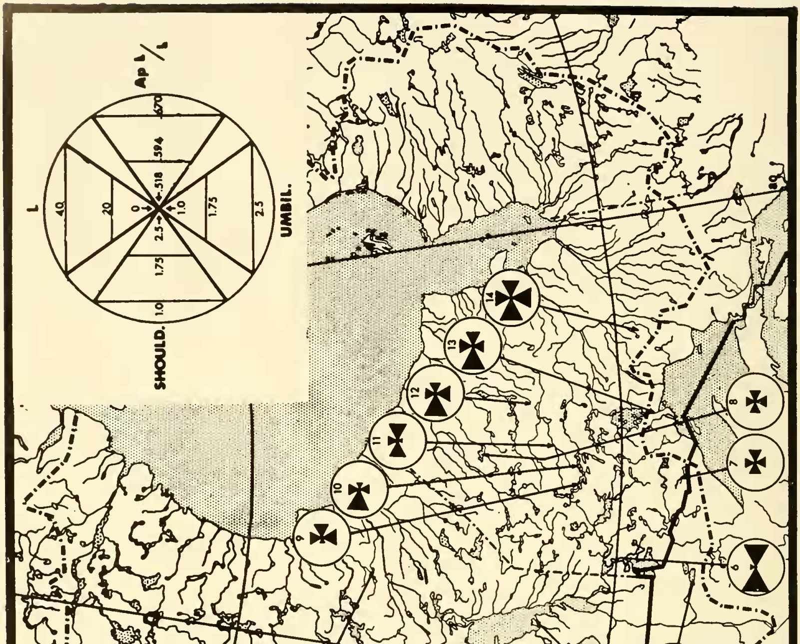


CHART 26. *Lymnaea catascopium* populations. For explanation see p 346.

TABLE 7. *Lymnaea catascopium* populations analyzed statistically.

No.	Locality
1	Lake 18 mi E of Chin Coulée, Alta.
2	Rocky Lake, 20 mi N of The Pas, Man.
3	Clear Lake, Man. (north shore).
4	Lake Winnipeg, island at entrance to Kinwow Bay, Man.
5	Lower Red Lake, 1 mi S of outlet into Red Lake River, Minn.
6	Lake of the Woods, Golf Course Bay, Lakeside Park, Kenora, Ont.
7	Basswood River Rapids, Rainy Lake District, Ont.—Minn. boundary.
8	Big Trout Lake, Ont.
9	Bamaji Lake, Ont., at outlet.
10	Lake St. Joseph, outlet, Rat Rapids, Ont.
11	Crow River, Attawapiskat District, Ont.
12	Mistassin Lake, Ont.
13	Nipigon River, Ont.
14	Nagagamisis Lake, 20 mi N of Hornepayne, Ont.
15	Lake Kakiska, N.W.T.
16	Lac Ile-à-la-Crosse, Sask.
17	Limestone Lake, Man.

Wil/Ap W	Maximum width of inner lip (measured parallel to Ap W) divided by Ap W.
Umbil.	Relative openness of umbilicus classed as 1, closed; 2, half closed by parietal callus; 3, entirely open.
Should.	Relative shouldering of whorls: 1, shoulders lacking; 2, moderate shoulders; 3, strong shoulders.
Sculp.	Strength of spiral sculpture: 1, weak; 2, moderate; 3, strong.
White Lines (Varices)	Strength and frequency: 1, none; 2, few or poorly shown; 3, many or strong.
Brown Ap.	Colour of aperture: 1, white; 2, light brown; 3, medium brown.
Colum. Plait	Development of columella plait: 1, none; 2, moderately developed; 3, heavy and strong.

The results of these measurements, statistically reduced, are shown on Charts 15 to 25. Conclusions which may be derived from these analyses are as follows:

(1) All characters analyzed show intra-population variability. The character showing the least such variability is length (L); those showing moderate variability are W/L, Ap L/L, Ap W/Ap L, Wil/Ap W, Should., White Lines (Varices), and Brown Ap.; and those showing extreme variability are Umbil., Sculp., and Colum. Plait.

(2) Inter-population variability is also relatively high. This variability is reasonably well related to geography in 4 characters (L, Ap L/L, Umbil., and Should.), less well related in 2 characters (Wil/Ap W and White Lines), and apparently unrelated to geography in the other characters.

(3) The characters customarily used to distinguish "*L. catascopium*" from "*L. emarginata*" show such considerable intra- and inter-population variability that they are not useful in delimiting species. Since no significant anatomical differences exist either, the 2 names are considered synonyms. The senior synonym is *Lymnaea catascopium* so that name

must be used (Clarke, 1968). Population samples from the type locality of *L. catascopium* are not available for analysis and this should be done, but for the present the concept of Say's original material as elucidated by Baker (1911) is accepted as correct.

(4) Mean values of the 4 characters best related to geography are combined on Chart 26. The results indicate in a more objective manner something which is visible on inspection of the specimens themselves, i.e., that population 6 (characterized by low values of L, Umbil., and Should., and high values of Ap L/L) is clearly different from the other populations and that populations 16 and 17 together (characterized by high values of L., Umbil., and Should., and low values of Ap L/L) are also quite different. These differences are also apparent from Charts 15, 17, 20, and 21. Population 6 and populations 16 and 17 are therefore regarded as distinct subspecies, viz., *Lymnaea catascopium nasoni* Baker and *L. c. preblei* Dall, respectively. They are discussed on subsequent pages.

(5) The character White Lines (Varices) is most prominently expressed in populations 2 and 3 from Manitoba. But it is also quite well expressed in some other populations and since there are no other characters whose geographical variation is concordant with this character these Manitoba populations are not considered taxonomically distinct. It is clear that genes responsible for the development of white collabral lines are more frequent in Manitoba populations, however.

(6) The character Wil/Ap W scores much higher in population 1 than in other populations. Again, however, other characters are not concordant and no subspecific status for this Alberta population is justified. It is possible that this population is closely related to populations occurring west of the Rocky Mountains. The taxonomic status of those populations needs examination.

(7) The other subspecies in this complex recorded by previous authors from the Canadian Interior Basin are either typological variants of normally highly variable populations or are otherwise not worthy of taxonomic distinction, as shown by analysis of the characters which have been used to distinguish them. These are therefore listed in the synonymy.

(8) Since all samples containing sufficient specimens to permit useful statistical analysis are from large bodies of water, and most are from large lakes with rocky substrates, no ecophenotypic relations are apparent from the charts. Large water bodies are the usual habitat of this species in any case. Smaller lots (not measured) do show some direct relationship between increased shell size and increased water body size, but very large lakes do not always produce very large shells. For example, specimens from Lake Winnipeg, Lake Winnipegosis, and Lake Manitoba are only medium-sized. Also, as discussed on subsequent pages, *L.c. nasoni*, the smallest subspecies of *L. catascopium*, occurs only in large lakes. But nevertheless the largest individuals of *L. catascopium* are always from large lakes, as pointed out by previous authors, and the smallest water bodies (e.g., side channels of the Attawapiskat River) appear to produce only small specimens. The probability appears great that genetic factors affect size independently, however.

Lymnaea catascopium nasoni Baker
Plate 23, Fig. 4; Map 63.

Lymnaea nasoni Baker, 1906: Notes on a collection of mollusks from the vicinity of Alpena, Michigan. *Trans. Acad. Sci., St. Louis, 16*(2): 12, pl. 1: 1–4. Type locality: "Thunder Bay Island, near Alpena, Michigan."

Limnaea woodruffi Baker, 1901: *Bull. Chicago, Acad. Sci., 2*: 229, fig. Type locality: "Lake Michigan, Oak Street, Chicago, Illinois."

Diagnosis: This subspecies is distinguishable from *Lymnaea catascopium* (*s. str.*) by its unusually small size, solid appearance, and wide, flaring aperture.

Description (of specimens from Lake of the Woods): Shells up to 2/5 inch in height, rotund, solid, yellowish- or purplish-brown, with expanded aperture and wide inner lip. Nuclear whorls with about 1¾ turns, small, dark brown, and satiny. Whorls about 4, rounded but not inflated, and forming a short, broadly acute spire. Sutures impressed. Body whorl dominant, occupying 80% to 90% of the total shell height, and subglobose in many specimens. Aperture ovate, expanded, white or brownish within and about ⅔ the height of the shell. Outer lip sharp but in many specimens thickened within by a low varix which is whitish or orange tinted. Inner lip broad, thickened, reflected, adherent to the parietal wall, and covering the umbilicus. Columella plait moderately developed. Sculpture consisting of impressed spiral lines and crowded collabral ridges which, in many specimens, assume a crescentric pattern between the spiral lines.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Type specimens of *Lymnaea nasoni* Baker (from Baker, 1911: 397).					
Length (L), mm	4	8·5 —10·5	9·62	—	—
W/L	4	0·63— 0·71	0·656	—	—
Ap L/L	4	0·67— 0·74	0·710	—	—
Ap W/Ap L	4	0·61— 0·72	0·669	—	—
Whorls	—	—	—	—	—
Type specimens of *Lymnaea woodruffi* Baker (from Baker, 1911: 398).					
Length (L), mm	3	10·5 —11·8	10·93	—	—
W/L	3	0·67— 0·72	0·692	—	—
Ap L/L	3	0·72— 0·81	0·764	—	—
Ap W/Ap L	3	0·56— 0·68	0·627	—	—
Whorls	—	—	—	—	—
Lake of the Woods, Kenora, Ont.*					
Length (L), mm	17	7·9 —10·3	8·87	—	—
W/L	17	0·60— 0·69	0·630	0·008	0·031
Ap L/L	17	0·59— 0·68	0·632	0·011	0·047
Ap W/Ap L	17	0·56— 0·70	0·628	0·005	0·029
Whorls	17	3·6 — 4·2	3·86	—	—

* For more complete measurements see population 6, Charts 15 to 25.

Records:

Winnipeg River system. Keats Lake (and Knife Lake?), Rainy River District, Ont. ("*Stagnicola* cf. *nasoni*", Baker 1939b: 92). Bay at Lakeside Park, Lake of the Woods, Kenora, Ont. (this survey).

Distribution: Lake Ontario at Niagara-on-the-Lake, N.Y. (Robertson & Blakeslee, 1948: 56); Lake Michigan; Lake Huron; probably Lake Superior (see "Remarks"); Lake Geneva, Wisconsin; parts of the Rainy River system; and Lake of the Woods.

Biology and Ecology: *Lymnaea catascopium nasoni* was found alive at only 1 locality, an enclosed bay of Lake of the Woods near the golf course at Lakeside Park, Kenora, Ontario. Here the snails were quite abundant and were found on black shale rocks at and slightly below the water surface. The dark snails were well camouflaged on the black rocks and those at the water surface were hardly distinguishable from bubbles. On July 18, 1969 many adults and numerous tiny juveniles occurred along with *Physa gyrina* and a few *Helisoma corpulentum*.

Baker (1911: 397) gives the habitat of "*Galba nasoni*" as "exposed shore of Lake Huron, where the water is daily forced into the pools." "*Galba woodruffi*" is known only from beach drift along Lake Michigan (Baker, 1911: 399). Nothing has been published on the anatomy or life history of *L.c. nasoni*.

In external aspect the soft parts appear similar to *Lymnaea catascopium* (*s. str.*) and *L. elodes*. Colour variation occurs but in general the tentacles and upper surface of the foot are pale grey-brown, the sole of the foot is grey, and the head is of a darker grey-brown flecked with tiny pale spots. Locomotion is quite rapid and of about the same speed as in *Physa gyrina*.

About 40 living specimens of *Lymnaea catascopium nasoni* were brought back to the laboratory and maintained in shallow (5 cm deep) water in an aquarium. They fed readily on lettuce and appeared to thrive. In mid-September several egg capsules were observed on the glass sides of the aquarium and on shells of living snails. The capsules were 5 to 6 mm in length, elongate-ovate, and bent in an open crescent configuration. The capsules contained from 8 to 20 pale yellow eggs and the lumen of the capsule was colourless. The capsules and eggs resemble those of *L. elodes*.

Radulae extracted from 2 specimens collected at Kenora were as follows. Tooth counts were taken across the widest portion of each radula.

Shell Length mm	Radula Size mm	Transverse Rows	Radula Formula
9·8	1·5 × 0·8	98	$\frac{15}{4\text{–}6}-\frac{3}{3}-\frac{10}{2}-\frac{1}{1}-\frac{10}{2}-\frac{3}{3}-\frac{14}{4\text{–}6}$ (28-1-27)
8·8	1·4 × 0·7	88	$\frac{12}{4\text{–}6}-\frac{3}{3}-\frac{10}{2}-\frac{1}{1}-\frac{10}{2}-\frac{3}{3}-\frac{12}{4\text{–}6}$ (25-1-25)

Remarks: This is another quite distinct morph of *Lymnaea catascopium* occurring in multiple populations in a definite geographical region and therefore qualified for subspecific status. It is probably closely related to "*Stagnicola walkeriana*" from Lake Superior and Lake Michigan (Baker, 1928a: 249). That morph is slightly larger and approaches other morphs of *L. catascopium* (*s. str.*), however, hence it has been synonymized under that subspecies. The whole problem needs further investigation.

Lymnaea catascopium preblei (Dall)
Plate 23, Fig. 3; Map 63.

Lymnaea (*binneyi* var.?) *preblei* Dall, 1905: *Land and fresh water mollusks of Alaska and adjoining regions.* Harriman Alaska Exped., *13*: 70, pl. 1: 1–2. Type locality: "English River [Churchill River], Manitoba [and] Knee Lake, Keewatin [northeastern Manitoba.]"

Diagnosis: Shell very large, swollen, thin, strongly sculptured, and with an acute, pointed spire.

Description: Shell up to 1⅔ inches high, variable, broad, pale brown, with pointed, acute spire, swollen whorls, coarse irregular sculpture, large aperture and open umbilicus. Nuclear whorls about 1½ in number, brownish, and large for members of the genus. Whorls 6, convex, shouldered in many specimens, strongly sculptured, and forming a short but acute and pointed spire. Sutures deeply impressed to channelled. Body whorl dominant and comprising sbout ¾ of the total shell length. Aperture ovate to subquadrate, large, slightly flaring, and about half the length of the shell. Outer lip thin, variously curved, and in some specimens with a reddish-brown collabral band within and close to the edge (one specimen from the type locality has 2 bands). Inner lip with a prominent callus which in its upper part is appressed to the body whorl but in its lower part is perpendicular to the plane of the aperture or reflected over (but not obscuring) the umbilicus. Columella plait variously developed, i.e., strong, weak, or absent. Umbilicus entirely open and deep. Sculpture consisting of prominent spiral ridges and low bands in many specimens, irregular malleations in some, and strong collabral lines and ridges. Periostracum thin, yellowish-brown, and moderately adherent.

Measurements:

For more extensive measurements see Charts 15 to 25, populations 16 and 17.

Feature	N	Range	Mean	$S.E._M$	S.D.
Type specimens (Dall 1905: 70).					
Length (L), mm	2	37, 38	37·50	—	—
W/L	2	0·62, 0·68	0·654	—	—
Ap L/L	2	0·61, 0·68	0·646	—	—
Ap W/Ap L	2	0·58, 0·73	0·654	—	—
Whorls	2	6, 5·5	5·8	—	—

Feature	N	Range	Mean	S.E.$_M$	S.D.
Lac Ile-à-la-Crosse, Sask.					
Length (L), mm	18	17·4 —27·2	19·11	—	—
W/L	18	0·70 — 0·78	0·726	0·004	0·020
Ap L/L	18	0·55 — 0·65	0·584	0·006	0·025
Ap W/Ap L	18	0·58 — 0·64	0·618	0·004	0·017
Whorls	16	5·2 — 5·7	4·81	—	—
Limestone Lake, Man.					
Length (L), mm	23	28·3 —41·7	35·29	—	—
W/L	23	0·62 — 0·74	0·661	0·005	0·026
Ap L/L	23	0·50 — 0·59	0·559	0·004	0·021
Ap W/Ap L	23	0·48 — 0·65	0·556	0·010	0·048
Whorls	23	5·6 — 6·8	6·14	—	—

Records:

Hayes River system. " Knee Lake, Keewatin " (55°03′N, 94°40′W, northeastern Manitoba) (Dall, 1905: 70). Knee Lake, Man., near outlet (55°10′N, 94°25′W), one dead specimen with flesh inside (this survey).

Nelson River system. Limestone Lake, Man. (56°35′N, 96°00′W), abundant (this survey).

Churchill River system. Lac Ile-à-la-Crosse, Sask. (1859, R. Kennicott!, also Dall, 1905: 70). " Clear Lake, N. Lat. 56°, Athabasca " (Baker, 1911: 451).* " English River " [=Churchill River, Man.] (Dall, loc. cit.).

Distribution: Known only from the Hayes, Nelson, and Churchill River localities (northern Saskatchewan and northern Manitoba) cited above.

Biology and Ecology: During this survey *Lymnaea catascopium preblei* was collected only from Limestone Lake and Knee Lake in northern Manitoba, both by use of aircraft. Empty shells were numerous at Limestone Lake on the beaches and sandy flats but only 1 specimen, a juvenile, was found alive. On the 1st visit there in 1965, no dredge was available for deep collecting and on the 2nd visit, in 1966, although a dredge had been carried along, strong wind and high waves prevented its use. Limestone Lake is large, mesotrophic, with shallow bays, and with a substrate of sand, muddy sand and large rocks. Vegetation (on August 2, 1965 and on July 22, 1966) was sparse and on the latter date the total hardness measured 138 p.p.m. The single living juvenile was found in a bay on muddy sand in about 2 feet of water. Adult specimens probably occur principally in depths exceeding 3 feet.

Knee Lake, the type locality of *Lymnaea catascopium preblei*, was visited on August 10, 1967 and collections were made in 3 areas. Knee Lake is a large, elongate, oligotrophic river-lake, with sparse vegetation, a substrate principally

* These specimens are in the United States National Museum (Cat. No. 43310) and are labelled 56°N, 108°W. I have been unable to locate a " Clear Lake " in that region on any map, old or recent, but if the location is correct it is near Lac Ile-à-la-Crosse, Sask.

of sand near shore and mud at greater depths, and water hardness of 70 p.p. m. $CaCO_3$, on the day it was visited. One large, freshly dead specimen was found in drift on a sandy, exposed beach through the combined efforts of 4 collectors over a ½ hour period. Another similar locality produced no *L. c. preblei* and a single dredge haul in 20 feet of depth was also negative. High water and lack of time impeded collecting efforts but at least the presence of this species at Knee Lake was confirmed.

No other ecological information is available but the records indicate that *Lymnaea catascopium preblei* is characteristic of large lakes and, possibly, of large rivers. No anatomical data are available.

The specimen from Knee Lake cited above was examined for radula characteristics. The shell is 41·7 mm long and the radula formula is approximately $\frac{19}{4}-\frac{6}{3}-\frac{14}{2}-\frac{1}{1}-\frac{14}{2}-\frac{6}{3}-\frac{19}{4}$ (39-1-39) when counted near the centre. The radula is 3·6 mm long, 1·4 mm wide and has 115 transverse rows of teeth.

Remarks: This is a northern peripheral group of populations of *Lymnaea catascopium* and it appears to be worthy of subspecific recognition. It is morphologically distinct and occupies a discrete geographical region. See the discussion under *L. catascopium* (*s. str.*) for further details.

Lymnaea elodes (Say)

Plate 12, Figs. 9, 10; Map 64.

Lymnaea palustris (Müller), *Galba palustris* (Müller), and *Stagnicola palustris* (Müller) of authors but not of Müller, 1774. Original citation of Müller's species is: *Buccinum palustre* O. F. Müller, 1774: *Vermium terrestrium et fluviatilium* . . . . [etc.], *2*: 131. Type locality: "In paludosis frequens" [no locality mentioned but Europe implied].

Lymneus elodes Say, 1821: *J. Acad. natr. Sci. Philad.*, *2*: 169 (Binney reprint, 1858: 66). Type locality: "Canandaigua Lake" [New York].

Lymneus desidiosus Say, 1821: op. cit., *2*: 169 (Binney reprint, 1858: 66). Type locality: "Cayuga Lake" [New York].

Limneus umbrosus Say, 1832: *Amer. Conchol.*, (4), pl. 31: 1 (new name for *Lymneus elongatus*, Say 1821 not *Limneus elongatus* Draparnaud, 1805). Type locality: (*L. elongatus* Say): "the ponds and tranquil waters of the Upper Missouri."

Lymnea Nuttalliana Lea, 1841: *Proc. Amer. phil., Soc.*, *2*: 33. Type locality: "Oregon."

Galba palustris alpenensis Baker, 1911: *Lymnaeidae of North America*. p 315, pl. 33: 26–33. Type locality: "Thunder Bay Island, near Alpena, Alpena Co., Michigan."

?*Stagnicola palustris ungava* Baker, 1933: *J. Wash. Acad. Sci.*, *23*(11): 523, fig. 1, bottom row, two figs. at right. Type locality: "Fort Chimo, Kuksoak [Koksoak] River, near Ungava Bay, Labrador [northern Quebec]."

Diagnosis: Shell medium to large, elongate, with rounded whorls, a moderate to heavy columella plait and coarse sculpturing.

Description: Shell up to 1¼ inches long, variable, moderately thin, light brown to blackish, spire medium to high, and with a heavy, spiral columella plait, a medium sized body whorl and aperture, and a dull to shining surface. Nuclear whorl finely punctate, shining, and rounded. Whorls rounded to somewhat flattened, 7 in number, and forming an acute, elongated spire with well impressed sutures. Spire whorls wider than high. Body whorl convex, subinflated, and occupying about ⅔ the length of the shell. Aperture more or less ovate and expanded, about ½ the length of the shell and in full-grown specimens thickened within by a brownish-purple varix. In some specimens the coloured band is present but no thickening is visible. Outer lip thin, rounded, and effuse in many specimens. Inner lip broad, with a heavy callus, and closely appressed to the parietal wall. Colu-

mellar plait heavy and spiral. Umbilicus partly open and narrow or closed by the parietal callus. Sculpturing coarse and consisting of numerous collabral lines, 1 to 3 growth rests, and many spiral lines with or without additional spiral bands or malleations or both. In many specimens tiny crescents occur between the spiral lines, their ends directed away from the aperture. Periostracum yellowish-brown to blackish-brown.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
2·5 mi S of Wetaskiwin, Alta.					
Length (L), mm	21	21·1 —32·4	26·65	—	—
Width (W), mm	21	10·3 —14·2	12·51	—	—
W/L	21	0·44— 0·50	0·470	0·012	0·053
Ap L/L	21	0·46— 0·53	0·498	0·005	0·023
Ap W/Ap L	21	0·45— 0·52	0·488	0·004	0·020
Whorls	20	6·2 — 7·1	6·70	—	—
Glaslyn, Sask.					
Length (L), mm	30	21·4 —28·2	23·67	—	—
Width (W), mm	30	9·9 —12·4	10·10	—	—
W/L	30	0·42— 0·48	0·456	0·003	0·015
Ap L/L	30	0·43— 0·50	0·468	0·004	0·020
Ap W/Ap L	30	0·42— 0·51	0·464	0·005	0·027
Whorls	29	6·2 — 7·3	6·49	—	—
6 mi SW of Oak Bluff, Man.					
Length (L), mm	30	14·6 —24·4	18·18	—	—
Width (W), mm	30	6·9 —11·8	8·42	—	—
W/L	30	0·42— 0·50	0·464	0·004	0·020
Ap L/L	30	0·46— 0·57	0·527	0·005	0·025
Ap W/Ap L	30	0·41— 0·53	0·467	0·005	0·028
Whorls	28	5·8 — 6·7	6·26	—	—
Near mission, Eastmain, Que.					
Length (L), mm	30	16·6 —27·9	23·40	—	—
Width (W), mm	30	9·1 —13·4	11·79	—	—
W/L	30	0·45— 0·57	0·506	0·005	0·028
Ap L/L	30	0·44— 0·56	0·496	0·005	0·029
Ap W/Ap L	30	0·44— 0·53	0·488	0·004	0·022
Whorls	25	5·8 — 7·0	6·34	—	—

Records:

There are approximately 500 collections of *Lymnaea elodes* in the National Museum of Natural Sciences from the region being considered. These collections are plotted on Map 64. West of the Precambrian Shield the species occurred at almost every station visited and therefore only marginal records in that region are cited. Within the Shield and to the north *L. elodes* is only sporadic, however, and all localities within that region are cited specifically. See "Remarks".

Ungava Bay drainage area. False River pond, Ungava Bay (1958, Fish. Res. Bd.!). Koksoak River, Fort Chimo, Quebec (type locality of *S. palustris ungava* Baker) (Baker, 1933: 523).

Southeastern Hudson Bay and eastern James Bay drainage areas. Pond, south end of Ross Island, Nastapoka Islands, N.W.T. (this survey). Surface pools south of cove, south side of The Hazard, Richmond Gulf, Que. (1950, J. L. Chamberlin!). Pond on island north of Cairn Island, Richmond Gulf. Inlet of Lower Char Lake, near Richmond Gulf. Pond near Clearwater River, ¾ mi E of Richmond Gulf (all this survey). Bloody Island Camp, Belcher Islands, N.W.T. (1958, Fish. Res. Bd.!). Side Channel of Fort George River, 12 mi E of Fort George, Que. Woods pool near mission, Eastmain, Que. Small ditch adjoining Lac Tiblemont, 11 mi S of Senneterre, Que. (all this survey).

Moose River system. Ditch at Baie la Sarre, Lake Abitibi, 3 mi WNW of Palmarolle, Que. Abitibi River, 17 mi N of Cochrane, Ont. Ditches 1½ mi N of Moosonee, Ont. (all this survey).

Albany River system. Klotz Lake, 30 mi E of Longlac, Ont. (rare) (this survey). Bamaji Lake, Ont. (1929, A. R. Cahn!).

Winisk River System. Small ponds in marsh, 6 mi E of Winisk, Ont. (this survey).

Severn River system. Severn Lake, north and south ends, Ont. (54°N, 94°40′W). Swamp near mission, Sandy Lake, Ont. (this survey).

Hayes River system. Muskeg near Red Sucker Lake, Man. (54°10′N, 93°57′W). Stull Lake, Ont. (54°29′N, 92°37′W) (both this survey).

Winnipeg River, Brokenhead River, Red River and Saskatchewan River systems, Lake Manitoba-Lake Winnipegosis drainage areas and Nelson River system. Occurs abundantly throughout the region (see Map 64) except not yet found on the Precambrian Shield in the upper Winnipeg River system or the Lake Winnipeg drainage area east of Lake Winnipeg.

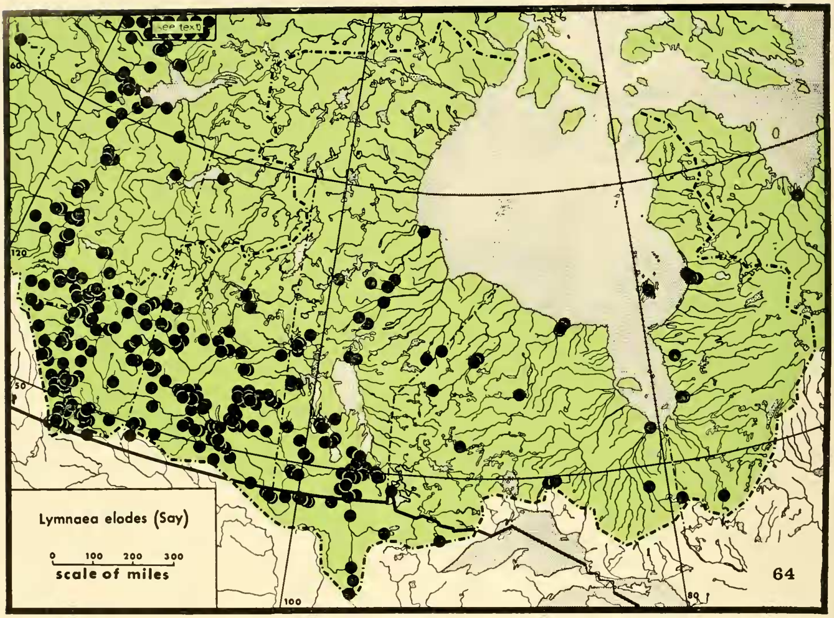
Churchill River system. Common in the Alberta and Saskatchewan parts of this sytem but less common in the Manitoba portion. In Manitoba it was found at Opachuanau Lake (56°44′N, 99°37′W), White Stone Lake (56°27′N, 97°30′W), Recluse Lake (56°55′N, 95°45′W), and Landing Lake, Churchill (all this survey).

Mackenzie River system. Common in the Peace, Liard, and Athabasca River systems; in the vicinity of Great Slave Lake; and in the Mackenzie River system as far as Fort McPherson, N.W.T. (67°27′N, 134°53′W) (1957, Fish. Res. Bd.!). Also Great Bear Lake, N.W.T. (Baker, 1911: 308).

Northern Arctic drainage area. Harbour at south end of "Husky Lakes" [=Eskimo Lakes], N.W.T. (68°52′N, 133°28′W) (1955, Fish. Res. Bd.!).

Distribution: *Lymnaea elodes* may be found from about 38°N (except south to near 33°N in California and New Mexico according to Baker, 1911: 308) north along both sides of Hudson Bay, in the east to Ungava Bay and in the west to near Churchill, Manitoba, and northwest to the mouth of the Mackenzie River and the Yukon River system. Fossil "*Stagnicola palustris*" are recorded from Kansan deposits in Kansas and later Pleistocene deposits elsewhere (La Rocque, 1963: 11, 12, etc.)

Biology and Ecology: The 146 collections of *Lymnaea elodes* made during the present survey, i.e., those for which consistently expressed ecological data were recorded, are from the following habitats: 19% are from large lakes, 6% from small lakes, 17% from permanent ponds, 6% from vernal ponds, 2% from backwaters, 5% from ditches and roadside sloughs, 5% from rivers over 100 feet wide, 6% from rivers 50 to 100 feet wide, 12% from rivers 25 to 50 feet wide, 13% from creeks 10 to 25 feet wide, 2% from brooks less than 10 feet wide, and 7% from swamps. Vegetation was thick at 46% of the collecting sites, of medium abundance at 23%, sparse at 28%, and absent at 3%. Bottom



sediments were recorded as composed partly or entirely of rock at 11% of the sites, gravel at 14%, sand at 32%, mud at 83%, and clay at 4%. In lotic environments the current was rapid at 15% of the sites, moderate at 28%, slow at 41%, and not perceptible at 16%.

Although these observations are influenced by the choice of collecting sites, they show clearly that *Lymnaea elodes* occurs in all kinds of habitats sampled. The species is most numerous where vegetation thrives but it can be found almost everywhere. This is in agreement with Baker (1911: 311) who also observed that the snail is omnivorous, feeding on living or dead vegetation and even on mammal carcasses.

The anatomy of this species has been described by Baker (1911: 305-307; 1928a: 213-218).

The radula formula reported is:

$$\frac{21}{4\text{-}6}\;\frac{4}{3}\;\frac{9}{2}\;\frac{1}{1}\;\frac{9}{2}\;\frac{4}{3}\;\frac{21}{4\text{-}6}$$

(34-1-34). Specimens collected during this survey from 7 widely separated localities were examined for radula characteristics and formulae of 27-1-26 to 34-1-33 were found. The highest count was derived from the largest specimen (23·2 mm) examined and the lowest value from the smallest specimen (9·2 mm). The ratios observed of numbers of lateral, intermediate, and marginal teeth were similar to those cited by Baker, but contrary to the data in Baker, the total numbers of teeth on each side of the central tooth often differ by 1 or 2 teeth.

Remarks: Hubendick (1951: 120) has indicated that European specimens of "*Lymnaea palustris*" may have 3 or more cusps on the 1st lateral teeth while

North American specimens [=*L. elodes*] have 2 cusps. Jackiewicz (1959) has shown that European lymnaeids with shells of the "*L. palustris*" morphology have diverse anatomical features. Walter (1968 and pers. comm.) has stated that Jackiewicz's data show that European "*L. palustris* (Müller)" is a composite of lymnaeiform, radiciform, and stagnicoliform species, which are all specifically different from "*L. palustris*" [=*L. elodes*] of North America. The status of the true *L. palustris* of Europe needs to be clarified, but the name is not applicable to the North American fauna and the name *Lymnaea elodes* (Say) must be used.

Lymnaea elodes is exceedingly variable and it is virtually impossible to distinguish it from *L. arctica* in some cases, at least by the shell alone. The 2 species appear to overlap broadly in the subarctic and arctic regions. In the Prairie Provinces *L. elodes* is abundant almost everywhere but in the vicinity of Hudson Bay and on the Precambrian Shield it is found only locally. The correlation between the intermittent occurrence of the species with the equally occasional occurrence of calcareous sediments in that region is striking as is the general absence of the species from areas in which such sediments have not been recorded. The comparatively large number of finds in the calcium-rich areas north of the Shield and close to the seacoast is also significant.

Some of the contrast in apparent abundance between the Prairie and Shield regions is probably because of collecting bias. The collections made by Dr. Richard Hartland-Rowe in Alberta in 1965 and 1966 were almost entirely from eutrophic habitats (roadside ditches, small ponds, etc.) as were most of those made during the present survey in Saskatchewan and Alberta in the rainy summer of 1965. Conversely a higher proportion of habitats visited in Quebec and Ontario during this survey were the large-lake and large-river types, less suitable for *L. elodes*. But numerous eutrophic habitats were also sampled on the Precambrian Shield and it is quite clear that the species really is uncommon to rare in most of the Shield area. The reports by Baker and Cahn (1931) and Baker (1939b) also show a general absence of *L. elodes* from this region. Baker's earlier (1911: 307) statement that it is absent from the Labrador region (part of the Precambrian Shield) also supports this conclusion even though, as shown above, that statement is not entirely correct.

The various taxa synonymized under *Lymnaea elodes* all appear to be non-geographically related variations of this polymorphic species. It is possible that *L. elodes ungava* represents a distinct subspecies but there is insufficient evidence available to justify a taxonomic separation. The specimens from False River pond near Ungava Bay (Pl. 23, Fig. 9) do exhibit the bulbous penultimate whorl observed by Baker in Fort Chimo specimens, but for the present those populations are tentatively retained under *L. elodes* (*s. str.*).

Lymnaea proxima Lea
Plate 23, Fig. 6; Map 65.

Lymnaea proxima Lea, 1856: *Proc. Acad. natr. Sci. Philad.*, p 80; 1866: *J. Acad. natr. Sci. Philad.*, *6*: 160, pl. 24: 74. Type locality: "Arroya, San Antonio, California."

Limnaea traski Tryon, 1863: *Proc. Acad. natr. Sci. Philad.*, p 149, pl. 1: 3. Type locality: "Mountain Lake, California."

Limnophysa tryonii Lea, 1865: (*in*) Tryon, *Amer. J. Conchol.*, *1*: 251. Type locality: "Arroya, San Antonio, Cal."

Stagnicola johnsoni F. C. Baker, 1934: *Can. Field-Naturalist*, *48* (4): 70. Refers to pl. 39,

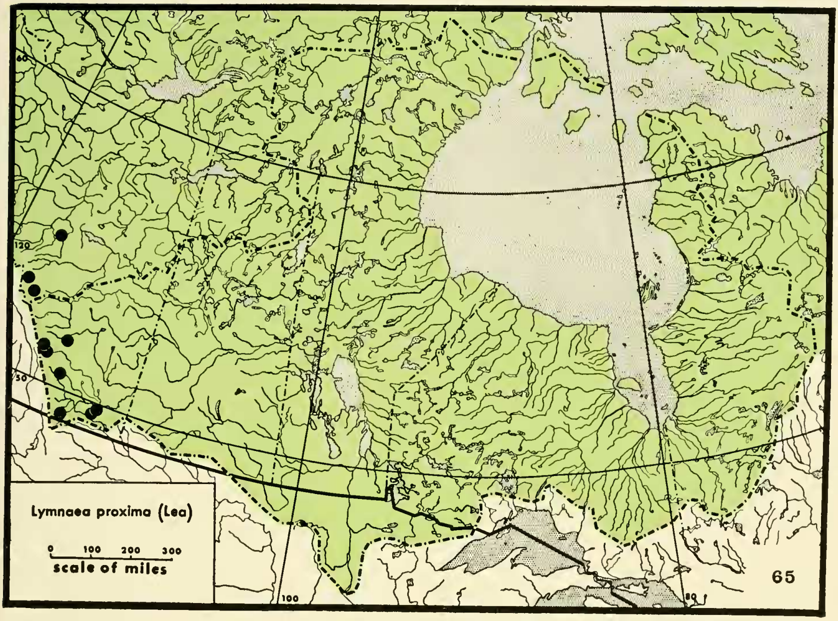
figs. 9, 10 in Baker, 1911 [types?]. Type locality: " Banff, Alberta."

Diagnosis: Shell medium-sized with large, rotund body whorl, acutely conical spire (" pinched " in many specimens), and reflected inner lip.

Description: Shell medium-sized (up to nearly 1 inch long), light brown to black, variable, moderately thick, with about 6 whorls, a rotund body whorl and a sharply acute spire. Nuclear whorls brown, satiny, and rounded. Spire acute, pyramidal, and narrow or of medium width; spire angle varying from about 30° to about 45°. Sutures impressed. Body whorl large, well rounded, and occupying about $\frac{2}{3}$ of the shell length. Aperture of moderate size, ovate, and continuous in many specimens. Outer lip thin and convex. Inner lip expanded, reflected over the umbilical region, and curved to rather straight but in most specimens without a columella plait. Umbilicus narrow but distinct in most specimens. Sculpture consists of rather coarse collabral lines and growth rests crossed by less distinct spiral lines.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Policeman's Creek, Canmore, Alta.					
Length (L), mm	30	15·0 —21·1	17·56	—	—
W/L	30	0·45 — 0·53	0·490	0·003	0·017
Ap L/L	30	0·48 — 0·57	0·512	0·004	0·020
Ap W/Ap L	30	0·44 — 0·52	0·467	0·003	0·017
Whorls	25	5·7 — 6·7	6·30	—	—
Stream near Banff Springs Hotel, Banff, Alta.					
Length (L), mm	30	10·3 —19·8	13·23	—	—
W/L	30	0·42 — 0·55	0·500	0·005	0·025
Ap L/L	30	0·45 — 0·55	0·498	0·005	0·025
Ap W/Ap L	30	0·43 — 0·57	0·509	0·005	0·029
Whorls	27	5·2 — 6·6	5·86	—	—
Maligne Lake, Jasper National Park, Alta.					
Length (L), mm	30	11·8 —22·2	14·59	—	—
W/L	30	0·46 — 0·56	0·515	0·005	0·027
Ap L/L	30	0·43 — 0·58	0·495	0·005	0·030
Ap W/Ap L	30	0·43 — 0·52	0·478	0·005	0·026
Whorls	30	5·5 — 6·5	5·99	—	—



Records:

Saskatchewan River system. South Saskatchewan River drainage area: 5·8 mi S of Wrentham, Alta. 3·5 mi W of Cardston, Alta. 1·5 mi S of Taber, Alta. 2·2 mi S of High River, Alta. (all 1966, R. Hartland-Rowe!.) Policeman's Creek, Canmore, Alta. (1964, R. W. Coleman!). Banff National Park, Alta. (4 localities, this survey; also 1963, Joyce Cook!). Roadside ditch, 5 mi S of Carstairs, Alta. (this survey).

Mackenzie River system. Maligne Lake and Edith Lake, Jasper National Park, Alta. (both 1964, R. W. Coleman!). Other localities in Jasper National Park (Mozley, 1938: 102). 1 mi N of Valleyview, Alta. (1963, Joyce Cook!).

Distribution: California to Wyoming north to British Columbia and Alberta. The precise limits of this species remain to be defined. There is no known fossil record.

Biology and Ecology: Only 2 collections of *Lymnaea proxima* were made during this survey, 1 from a roadside ditch with thick vegetation and mud bottom and the other from a small brook (heated to about 75°F by warm springs at Banff, Alta.) with a rapid current, moderate vegetation (moss and algae), and a stony bottom. Mozley (1938: 102, under *L. traskii*) writes that " This species is usually found on open shores of large lakes but has also been collected in ponds. " Baker (1928a: 360) gives the ecology of *L. proxima* as " in mountain streams and small lakes, generally at high altitudes. "

No information has been found in the literature regarding the radula of *Lymnaea proxima*. Radulae from 5 speci-

mens collected during this survey were examined and were found to be variable but similar to those of *L. elodes*. Their formulae are given below.

Catalogue Number	Locality	Shell Length mm	Radula Formula
32243 A	Brook near Banff Springs Hotel, Banff, Alta.	19·9	$\frac{21}{3\text{–}5}-\frac{5}{3}-\frac{10}{2}-\frac{1}{1}-\frac{10}{2}-\frac{5}{2}-\frac{19}{3\text{–}5}$ (36–1–34)
32243 B	Brook near Banff Springs Hotel, Banff, Alta.	16·4	same formula
32886 A	Policeman's Creek, Canmore, Alta.	19·3	$\frac{19}{3\text{–}5}-\frac{5}{3}-\frac{12}{2}-\frac{1}{1}-\frac{12}{2}-\frac{5}{3}-\frac{18}{3\text{–}5}$ (36–1–35)
32886 B	Policeman's Creek, Canmore, Alta.	18·7	$\frac{17}{4\text{–}5}-\frac{3}{3}-\frac{11}{2}-\frac{1}{1}-\frac{11}{2}-\frac{3}{3}-\frac{17}{4\text{–}5}$ (31–1–31)
37962 A	3·5 mi W of Cardston, Alta.	21·7	$\frac{17}{4}-\frac{3}{3}-\frac{11}{2}-\frac{1}{1}-\frac{11}{2}-\frac{3}{3}-\frac{16}{4}$ (31–1–30)

Remarks: The best statement of differences between *Lymnaea proxima* and the closely-related *L. elodes* has been given by Baker (1911: 361), as follows: "*Proxima* resembles certain long-spired forms of *palustris* [=*elodes*] from which it may be distinguished by its more *convex body whorl, longer and more regularly conic spire and rounder aperture, and more rapidly enlarging whorls.*"

Specimens from the Canadian Interior Basin were compared with the type lot of *Lymnaea proxima* Lea in the United States National Museum. Although not identical, the lots were similar and the differences between them were no more extreme than those which are often found between different populations of normally polymorphic lymnaeids.

Lymnaea reflexa (Say)
Plate 23, Figs. 7, 8; Map 66.

Lymneus reflexus Say, 1821: *J. Acad. natr. Sci. Philad.*, *2*: 167; *Amer. Conchol.* (etc.), pl. 31: 2 (1832) (Binney reprint, 1858: 65, pl. 31: 2). Type locality: "Inhabits Lakes Erie and Superior."

Lymnaea exilis Lea, 1834: Observations on the Naiades (etc.). *Trans. Amer. phil. Soc.*, *5*(N.S.): 114, pl. 19: 82. Type locality: "Ohio."

Lymnaea kirtlandiana Lea, 1841: Continuation of, Mr. Lea's Paper (etc.). *Trans. Amer. phil. Soc.* *2*(1): 33. Type locality: "Poland, Ohio."

Limnaea lanceata Gould, 1848: [Report of meeting held October 18, 1848]. *Proc. Boston Soc. natr. Hist.*, *3*: 64. Type locality: "North shore of Lake Superior, 'Pic Lake'."

Limnaea zebra Tryon, 1865: Descriptions of New Species of North American Limnaeidae. *Amer. J. Conchol.*, *1*: 228, pl. 23: 4. Type locality: "Minnesota."

Diagnosis: Shell medium-sized, very elongate, slender, with flattened whorls, in many specimens with zebra-like light and dark collabral bands and in most specimens with the aperture less than ½ of the length of the whole shell.

Description: Shell medium-sized (up to about 1½ inches long), rather thin, much elongated, narrow, with flattened whorls and in most specimens with an aperture

whose length is less than half the total shell length. Nuclear whorls satiny, about $1\frac{1}{2}$ in number, and turreted. Spire whorls separated by well-marked sutures. Whorls about 7. Body whorl and penultimate whorl much elongated. Aperture long, reflexed in many mature specimens, narrowed and acutely angled at the apex and rounded and subtruncated at the base. In many specimens the aperture rim is made continuous by an elevation of the inner lip. Outer lip sharp and thin at the edge, thickened internally with a varix which is brown or purplish in colour. Inner lip narrow, thickened or thin, and reflected over the umbilicus leaving a small chink visible or completely obscuring the umbilicus. Columella oblique and in adult specimens with a prominent plait which ascends spirally into the body whorl. Surface light brown to blackish brown, with numerous collabral ridges and, in many specimens, with alternating light and dark collabral bands. Fine sculpture consists of closely spaced collabral wrinkles and numerous shallow, spiral grooves.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Pools ½ mi SE of Star Lake, Whiteshell Provincial Park, Man.					
Length (L), mm	22	15·9 —25·0	18·96	—	—
Width (W), mm	22	6·0 — 9·2	7·25	—	—
W/L	22	0·33 — 0·40	0·366	0·004	0·020
Ap L/L	22	0·43 — 0·54	0·490	0·006	0·029
RZ *	22	1·0 — 3·0	2·02	0·12	0·57
Whorls	22	4·0 — 6·2	5·50	—	—

RZ (relative "zebration") is an estimate of the extent to which the surface is covered by zebra-like alternating dark and light collabral bands. It is recorded as follows: 1, stripes absent; 2, stripes present but covering only about one-half of the shell; 3, stripes covering the whole shell.

Records:

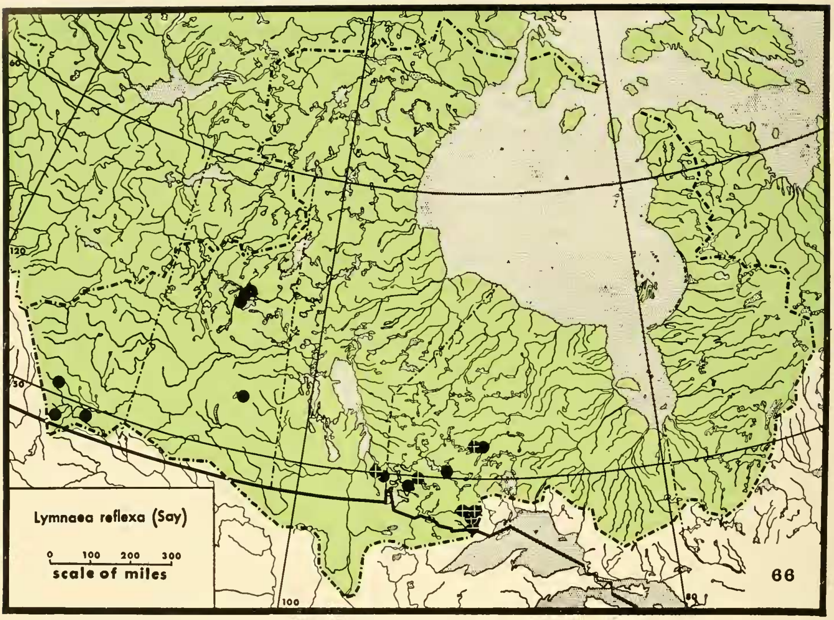
Since most lots of specimens examined are very small, values of N, L, W, Ap L/L, and RZ are included below with the localities. As usual, all measurements are in mm.

Albany River system. Cat Lake, Ont. (N=1, L=14·6, W=5·0, Ap L/L=0·507, RZ=2·0). Bamaji Lake, Ont. (N=1, L=15·4, W=5·1, Ap L/L=0·448, RZ=1·5) (both 1929, A. R. Cahn!). Pashkokogan Lake, Ont. Bamaji Lake outlet, Ont. (both Baker & Cahn, 1931: 53).

Winnipeg River system. Cat Lake, Lac des Mille Lacs, Mercutio Lake, Snodgrass Lake, rapid water between Saganagons and Kahnipiminanikok [Kawnipi] lakes, lake west of West Lake and north of South Lake, Iron Lake, Knife Lake, and Little Knife Lake, western Ontario (all Baker, 1939b: 92, as "*Stagnicola lanceata*"). Old Woman Lake, 35 mi S of Kenora, Ont. (N=2, L=19·1, 18·0; W=7·0, 6·0; Ap L/L=0·473, 0·466; RZ=2·5, 2·5). Abram Lake, Sioux Lookout, Ont. (N=1, L=11·9, W=5·0, Ap L/L=0·500, RZ=1·5). (both this survey). Canyon Lake, Ont. (49°58′N, 93°40′W) (Mozley, 1938: 102). Pools ½ mi SE of Star Lake, Whiteshell Provincial Park, Man. (see "Measurements") (1964, F. R. and J. C. Cook!). Whiteshell River, several localities, Man. Lake, Brereton, Man. (both Mozley, 1938: 102).

Quill Lakes drainage area. Little Quill Lake, Sask. (N=1, L=18·8, W=6·0, Ap L/L=0·468, RZ=1·0; another specimen broken, RZ=1·0) (1920, collector?).

Saskatchewan River system. 4·7 mi W of Wrentham, Alta. (N=2, L=18·5; W=8·1,



6·6; Ap L/L=0·432, 0·466, RZ=1·0, 1·0). 13·5 mi W of Cayley, Alta. (N=1, L=22·7, W=9·7, Ap L/L=0·408, RZ=1·0), (both 1966, R. Hartland-Rowe!).

Churchill River system. Nemeiben River, 2 mi N of La Ronge, Sask. (N=1, L=18·6, W=6·6, Ap L/L=0·473, RZ=1·5). Midway Lake, 13 mi N of La Ronge (N=1, L=26·1, W=9·6, Ap L/L=0·414, RZ=1·0). Twin Lake, 35 mi N of La Ronge (N=3, L=15·1, 16·5, 17·3; W=6·6, 6·7, 7·0; Ap L/L=0·470, 0·503, 0·497; RZ=2·5, 2·0, 3·0) (all this survey).

Distribution: Ohio-Mississippi drainage area north of about the 37th parallel. Great Lakes-St. Lawrence River system throughout, including artificially connected waterways in New York. Canadian Interior Basin in several disjunct areas (see Map 66). Recorded from Nebraskan deposits in Kansas (Taylor, 1960: 39) and in later Pleistocene deposits there (La Rocque, 1963: 16, 17, etc.).

Biology and Ecology: According to Baker (1911: 339), *Lymnaea reflexa* occurs " in creeks, ponds, lakes and rivers in sheltered localities, attached to floating debris, submerged vegetation, stones, etc.; also found on decaying fruit, vegetables, etc. In many localities *L. reflexa* is found in small ponds, ditches, beside roads and railway tracks and in sloughs and other bodies of water which dry up more or less in summer. " Under " *Galba lanceata* ", here considered synonymous with *L. reflexea*, Baker (1911: 352) gives its usual habitat as " swampy areas where there is a quantity of vegetation such as *Typha* and the pond scums, in which situation it may be found on floating logs or in the vegetation. " Mozley (1938: 102) writes " *Habitat*. Marshes, particularly those near streams or large bodies of water. "

During this survey *Lymnaea reflexa* was found in 5 localities: in 1 large lake, in 3 small lakes, and in a rapidly-flowing river about 50 feet wide. Bottom deposits were various (mud, sand, gravel, or rocks or any combination of these) and vegetation was sparse at 2 localities, moderate at 1, and thick at 2. The specimens from Star Lake, Manitoba, were found in an area of small, shallow vernal puddles and pools. Clearly, this species occurs in a very wide range of habitats.

The anatomy and radula of *Lymnaea reflexa* are similar to that of *L. elodes* (Baker, 1911: 335; 1928a: 223; Hubendick, 1951: 102; Walter, pers. comm.). The radula formula is reported as 40-1-40 with the first laterals bicuspid and the marginals approximately pentacuspid (see Baker, 1911: 335 for details). Bovbjerg (1965) found that locomotion was random, that various algae and vascular plants (and also liver) were readily eaten, and that, as in other herbivorous snails, contact chemoreception was good, but distant chemoreception was not evident.

Remarks: Even though Hubendick (1951: 119-122, fig. 303) and Walter (pers. comm.) have found no differences in anatomy between *Lymnaea reflexa* and *L. elodes*, on the basis of shell characters and zoogeography I believe that the 2 taxa are probably not synonymous. It is relatively certain that the several related species recognized by Baker (see La Rocque, 1953: 278-281) are not valid, however, as indicated in the above synonymy. Breeding experiments are needed to establish firmly the relationships of *L. reflexa* and *L. elodes*.

Superfamily Physacea

Following Taylor (ms.) and my own independent judgement this superfamily is here recognized as distinct. It contains only the Family Physidae, described below.

Family PHYSIDAE Fitzinger

Physoidea Fitzinger, 1833: *Beiträge zur Landeskunde Oesterreich's unter der Enns.*, *3*: 110. Type genus: *Physa* Draparnaud.

Shells small to rather large, thin or slightly thickened, hyperstrophic (i.e., sinistral), conispiral and non-umbilicate. Aperture large, angled above and rounded below. Spire short to moderately produced. Surface smooth or with well-marked microsculpture. Monoecious (with facultative self- and cross-fertilization) and phytophagous.

" Animal sinistral, having the pulmonary, genital and excretory orifices on the left side; tentacles slender, cylindrical; foot narrow, pointed behind; jaw single, arcuate, with a vertical fibrous accessory process on the superior margin; radula with the teeth arranged in oblique [chevron-shaped] rows. Central tooth wide, base with projecting processes before and behind, multicuspid; laterals obliquely bent, comb-like, multicuspid, with a peculiar process at their external angle. " (Walker, 1918: 15).

This family is world-wide and its geologic range extends from Upper Carboniferous (?) or Jurassic to Recent. Three genera are recognized: *Physa* Draparnaud, *Aplexa* Fleming, and *Stenophysa* von Martens, the latter now occurring only in Central and South America.

KEY TO SPECIES AND SUBSPECIES OF PHYSIDAE

1. Shell relatively narrow, W/L less than 0·50 (except in some juvenile specimens) and surface glossy. Mantle margin without digitations . . . . *Aplexa hypnorum* (p 383, Pl. 13, Fig. 2; Pl. 24, Fig. 11)
   Shell relatively wider, W/L more than 0·50 and surface may be smooth but not glossy.

Mantle margin with prominent digitations extending over parietal and columellar regions (*Physa* spp.) 2

2. Apex pointed, body whorl rounded, length up to about 24 mm 3

Apex rounded and blunt, body whorl laterally flattened, length up to about 12 mm 4

3. Length of adults less than 10 mm, spire short, apex not reddish. Only in the vicinity of Banff, Alta . . . . . *Physa johnsoni* (p 381, Pl. 24, Fig. 10)

Length of adults more than 10 mm, spire short to medium long, apex reddish. Widespread and abundant . . . . . *Physa gyrina* (p 373, Pl. 13, Fig. 1; Pl. 24, Figs. 7–9)

4. Penultimate or next preceding whorl, or both, largely exposed (i.e., not mostly enveloped by succeeding whorls) causing them to appear disproportionately high. Widespread in southern Canada . . . . *Physa jennessi skinneri* (p 368, Pl. 24, Figs. 1, 2)

Penultimate and next preceding whorl largely enveloped by succeeding whorls and not disproportionally high 5

5. Ap L/L of most specimens exceeding 0·75. Shell and soft parts white or whitish. Columellar mantle digitations about 4. Vicinity of Jasper, Alta. and nearby parts of the Mackenzie River system . . . . . *Physa jennessi athearni* (p 365, Pl. 24, figs. 4–6)

Ap L/L of most specimens less than 0·75. Shell and soft parts brown or grey, not white. Columellar mantle digitations about

6. Widespread in the western Arctic and near Hudson Bay . . . . *Physa jennessi jennessi* (p 362, Pl. 24, Fig. 3)

Genus *Physa* Draparnaud

Physa Draparnaud, 1801: *Tableau des Mollusques terrestres et fluviatiles de la France*. Type species: *Bulla fontinalis* L., by subsequent designation (Children, 1823: *Quart. J. Sci., Lit. & Art*, *15*: 243). Placed on the Official List of Generic Names in Zoology (Name No. 460) by Opinion 363 of the International Commission on Zoological Nomenclature, 1955.

Shell sinistral, small to medium-sized, subovate, and with or without fine spiral sculpture. Soft parts as in the other genera of Physidae except that in *Physa* the edge of the mantle bears many prominent lobes or digitations which extend partly over the shell, especially in the columella region.

Twenty-six species and subspecies of *Physa* have been listed from Canada (La Rocque, 1953: 297-301) and scores of others have been described from elsewhere. Most of these are probably invalid. The genus is abundant and world-wide in distribution. *Physa* appears to be more tolerant of pollution than most other freshwater animals and sometimes occurs in great abundance in mildly-polluted water, presumably because fish and other animals which feed on *Physa* do not live in such habitats. Geologic range: Upper Carboniferous (questionable) or Jurassic to Recent (Zilch, 1959: 91).

Physa jennessi jennessi Dall
Plate 24, Fig. 3; Map 67.

Physa jennessi Dall, 1919: *Rept. Can. Arctic Exped.* 1913–18, *8*(A): 20A, pl. 2: 2. Type locality: "Ponds near Bernard Harbour, [N.W.T.] rare."

Diagnosis: Shell about $\frac{1}{3}$ inch tall, apex acute but rounded, spire short, body whorl roundly shouldered and laterally flattened, parietal callus broad, and sculpture consisting of irregular growth lines and fine spiral striae.

Description: "Shell small, thin, of four whorls, of a dull amber yellow without a darker streak behind the outer lip; apex rounded, rather blunt, surface polished, with occasional incremental irregularities and a microscopic spiral striation obsolete in places; spire shorter than the aperture, the last whorl much the largest, the suture not deep, the whorls moderately rounded; outer lip sharp, inner lip slightly erased and whitened; pillar straight, thickened where it meets the body, with a little depression behind it. Length 8; length of aperture 5; max. diameter 5 mm." (Dall, 1919: 20A).

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Pool on island, 35 mi NE of Poste de la Baleine (Great Whale River), Que.					
Length (L), mm	6	5·8 —8·9	7·43	—	—
Width (W), mm	5	3·1 —4·7	3·96	—	—
W/L	5	0·49—0·58	0·522	—	—
Aperture length (ApL), mm	6	4·4 —6·0	5·28	—	—
ApL/L	6	0·67—0·75	0·708	0·011	0·027
Whorls	6	3·9 —5·0	4·33	—	—
Creek outlet, Bernard Harbour, N.W.T. (*P. jennessi* paratypes).					
Length (L), mm	20	6·4 —8·9	7·54	—	—
Width (W), mm	20	3·4 —5·3	4·29	—	—
W/L	20	0·53—0·79	0·570	0·009	0·040
Aperture length (ApL), mm	20	4·1 —5·8	4·93	—	—
ApL/L	20	0·61—0·75	0·654	0·008	0·036
Whorls	19	4·2 —4·8	4·24	—	—

Records:

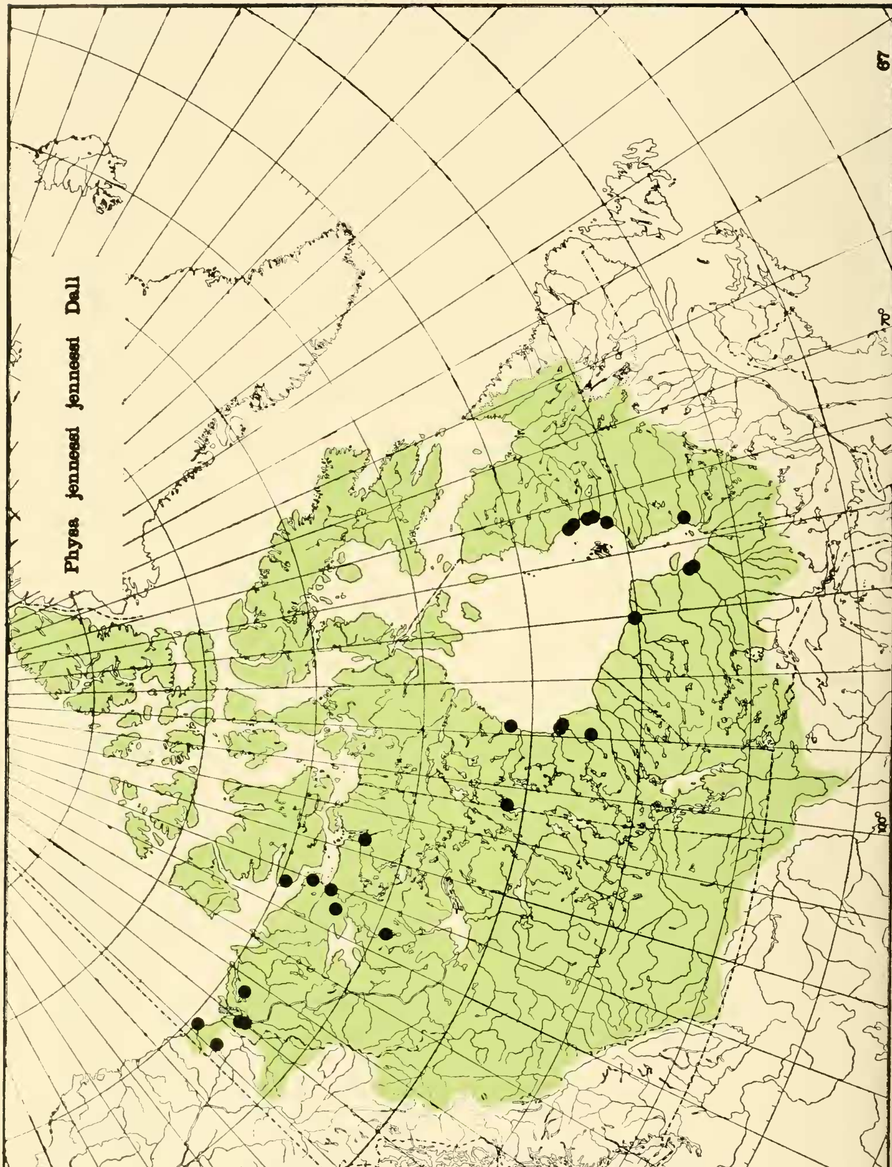
Eastern Hudson Bay and James Bay drainage areas. Lake, south half of Mowat Island and ponds on Anderson Island and Ross Island, all in Nastapoka Islands group. Rock pool, eastern end of The Hazard, Richmond Gulf, Que. Rock pools on island at " Boat Opening," 35 mi NE of Poste de la Baleine (Great Whale River), Que. Woods pool, Eastmain, Que. (all this survey). " Grey Goose Island," James Bay (1914, W. E. Walton!).

Western Hudson Bay drainage areas. Small lake at Devil's Gut, S of Albany Island, Albany River estuary (albino specimens). Small ponds in muskeg, 6 mi E of Winisk, Ont. Small brook 5 mi E of Winisk. Owl Lake, Man. (56°22′N, 94°35′W). Rock pool near Hudson Bay, Churchill, Man. Landing Lake, Churchill. Goose Creek and mouth of Goose Creek, 7 mi S of Churchill (all this survey). Pond, west side of Churchill, Man. Tundra pools, Fort Churchill, Man. (both 1929, F. Johansen!). " Lake c ", Eskimo Point, N.W.T. (1930, G. R. Roberts!).

Northern Arctic drainage areas. Unnamed small lake W of Bathurst Inlet, N.W.T. (66°32′N, 107°42′W) (1962, W. Blake, Jr.!) Coppermine Bluff, spring run-off pool, N.W.T. (67°49′N, 115°06′W) (1957, Fish. Res. Bd.!). Dismal Lakes, N.W.T. (67°13′50″N, 116°32′40″W) (1959, Fish. Res. Bd.!). E of Bernard Harbour, N.W.T.; creek and lake at Bernard Harbour; and creek outlet behind Bernard Harbour (holotype and paratypes of *P. jennessi*). Creek " between Cape Baring and Point Pullen ", Wollaston Peninsula, Victoria Island, N.W.T, (all 1915–16, Can. Arctic Exped.!). Harbour at south end of Husky [=Eskimo] Lakes, N.W.T. (68°52′N, 133°28′W) (1955, Fish. Res. Bd.!). Aklavik, N.W.T. (1957, Fish. Res. Bd.!). Lakes 30 mi S of Aklavik (date?, W. Kennedy!). Pond on Herschel Island Y.T. (1914–15, Can. Arctic Exped.!). Unnamed lake, Y.T. (68°03′N, 139°55′W) (1960, D. E. McAllister!).

Distribution: Currently known only from localities close to Hudson Bay and James Bay and in the Western Arctic in the vicinity of Bathurst Inlet, Coppermine River, southern Victoria Island, the Mackenzie Delta, and northernmost Yukon Territory.

Biology and Ecology: The 14 lots of *Physa jennessi jennessi* collected during


Physa jennessi jennessi Dall

this survery were from the following habitats: 3 are from small lakes, 3 are from permanent ponds, 1 is from a subarctic woods pool which may be vernal (Eastmain, Que.), 1 is from a pool in muskeg, 3 are from small to medium-sized, slow-flowing streams, and 3, from both sides of Hudson Bay, are from small pools on the tops of large, flat boulders within 100 yards of the shore of Hudson Bay. These pools were only a few square yards in area, not more than 1 foot deep, and were entirely without soil or vegetation other than periphytonic algae. In the other localities vegetation was sparse to abundant and bottom sediments were of rocks or mud or both.

According to Johansen (*in* Dall, 1919: 24A) on July 5, 1916 " many of the common fresh-water snails (*Aplexa*) and a few *Lymnaea* [=*Lymnaea kennicotti*] and *Physa* [=*P. j. jennessi*] were collected in the shallow bights at the outlet of the big creek from the large lake in valley back of the harbour [Bernard Harbour, N.W.T.]. "

Available information indicates that *Physa jennessi jennessi* is a true arctic species which occurs in very small rock or tundra pools, in larger ponds on tundra, in creeks, and in lakes. Its most common associates in the vicinity of Hudson Bay are *Lymnaea arctica* and *Gyraulus parvus*.

One broken specimen about 9 mm long from near Husky Lakes, N.W.T. had a radula 2·2 mm long and 1·7 mm wide. The radula bears 67 chevron-shaped rows of teeth, each with approximately 123 lateral teeth on each side of the central tooth. The central tooth is very small and has 5 cusps; the lateral teeth have 7 to 8 large cusps and the middle to outer laterals bear a single minute cusp between most of the large cusps.

Specimens in alcohol have a pale brown head, foot, and mantle edge. The mantle surface visible through the shell is dark grey with pale spots. Mantle digitations are of slightly less than medium-size and there are about 6 columellar and 4 parietal digitations.

Remarks: There are striking similarities between *Physa jennessi jennessi* and *Lymnaea arctica* (Lea). Both may be distinguished in the field from their most widespread and abundant boreal relatives (*P. gyrina* and *L. elodes*), by being smaller, more heavily sculptured, and having a much wider parietal callus. Both *P. j. jennessi* and *L. arctica* are similar in distribution (with *L. arctica* the more abundant) and to some extent in habitat. It appears probable that both survived and speciated in the Beringian Refugium during the Pleistocene and that both species may have invaded the arctic shores of Hudson Bay from Beringia after the recession of the Wisconsin glaciation.

Physa jennessi jennessi differs from *P.j. skinneri* principally in that the penultimate whorl of *P. jennessi* (*s. str.*) is not disproportionately attenuated while in adults of *P. j. skinneri* that character is pronounced. *P. j. athearni* has a more obtuse spire but the apex is rather more pointed. It also lacks pigmentation of the shell and the soft parts.

Physa jennessi athearni (new subspecies)
Plate 24, Figs. 4-6; Map 68.

Diagnosis: Shell about $\frac{1}{3}$ inch tall; white; subglobose; with short, bluntly pointed spire; roundly shouldered whorls; and dominant, peripherally flattened body whorl. Soft parts white, without mantle spots, and with about 8 small mantle digitations, 4 projecting feebly on to the columella and 4 on to the parietal wall.

Description: Shell sinistral, variable, subglobose, pale yellowish-white, thin, and up to about 7 mm long and 5 mm wide and with 4 whorls. Nuclear whorl large, rounded, about 0·7 mm wide and elevated well above the second whorl. Spire short, about $\frac{1}{6}$ the length of the shell, acute to slightly obtuse, and with the first 3 whorls enlarging evenly, flatly rounded, and separated by impressed sutures. Sutures bordered below by a narrow, paler band. Body whorl capacious, inflated, dominant, roundly shouldered above and flattened centrally giving the shell a characteristic, misshapen appearance. Aperture large, pendulous, acute above, flattened laterally, and broadly rounded below. Columella sigmoid and parietal callus narrow above and broader below Umbilicus absent or indicated by a tiny slit. Sculpture consisting of fine, crowded collabral lines and wrinkles and, on some specimens, a single whitish, narrow growth rest on the body whorl, or impressed, microscopic spiral lines which cross and interrupt the collabral wrinkles or with both kinds of sculpture.

This subspecies differs conspicuously from both *Physa jennessi jennessi* and *P. j. skinneri* in its broader, more capacious body whorl and in the whitish-colour of its shell and soft parts. It differs from *P. j. skinneri* also in its shorter, more regular spire and its fewer and smaller mantle digitations.

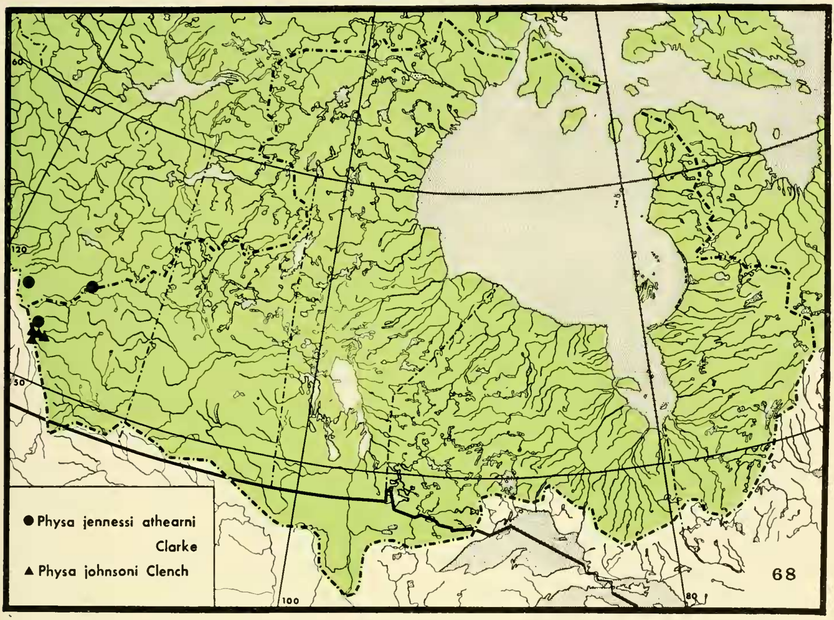
Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Horseshoe Lake, 10 mi SE of Jasper, Alta. (type lot).					
Length* (L), mm	34	3·9 —7·6	5·89	—	—
W/L	34	0·52—0·65	0·586	0·005	0·031
Ap L/L	34	0·71—0·94	0·808	0·011	0·063
Whorls	34	2·0 —4·2	3·64	—	—

* The nuclear whorl is eroded in most specimens and length measurements were corrected in such cases by adding 0·2 mm.

Allometry is not a factor within the sample tabulated; the largest and smallest specimens have intermediate values of W/L and ApL/L and no shifts in these values with increasing size occur. The largest specimen was anomalous, however, and had an unusually expanded body whorl. Its measurements, not included above, are L 7·7; W/L 0·80; ApL/L 0·84; whorls, 3·7. Two specimens were broken and could not be measured.

Types: The holotype (NMC 46384) is preserved in alcohol in the Mollusc Collection of the National Museum of Natural Sciences, National Museums of Canada. It is 6·7 mm long, 3·8 mm wide, 5·2 mm in aperture length, and has 3·7 whorls. Paratypes, both dry and with preserved softs parts, are deposited in the National Museum of Natural Sciences (NMC 32483); the United States National Museum; the Museum of Zoology, University of Michigan;



and the Museum of Comparative Zoology, Harvard University. Measurements of the whole population sample, however, are given above.

This subspecies is named in honor of Mr. H. D. Athearn of Cleveland, Tennessee. Mr. Athearn collected most of the known material of this new subspecies. He has also been an enthusiastic and knowledgeable specialist in freshwater molluscs, and a friend and colleague, for many years.

Records:

South Saskatchewan River system. Johnson Lake, near Two Jack Lake Road, Banff National Park, Alta. (2 specimens) (June 17, 1964, Persis C. & Richard W. Coleman!).

Athabasca River system. Horseshoe Lake, about 10 mi SE of Jasper, Alta. (holotype and 36 paratypes) July 21, 1965. Marsh 1 mi W of Dapp Creek, 4·5 mi W of Rochester, Alta. (20 specimens) July 16, 1965 (both H. D. Athearn!, this survey).

Distribution: Small lakes in the Banff-Jasper Region of the Rocky Mountains, western Alberta; also downstream from the Jasper locality, in a marsh, in the Athabasca River system.

Biology and Ecology: Available information indicates that *Physa jennessi athearni* occurs in small to medium-sized lakes and in marshes with open water. Substrates observed are rock and gravel but vegetation abundance was not noted.

The soft parts of all specimens in the type lot and in the lot from Johnson Lake, Banff National Park, are whitish. Those from near Rochester, Alta. are pale but pigmented and showed white mantle spots on a grey background through the shell.

The radulae of 3 paratypes are as follows:

Specimen No.	Shell Length mm	Lateral Teeth (One side, three rows)	No. of Rows	Radula Length mm	Radula Width mm
32483-4	6·6	160, 163, 170	75	1·6	1·2
32483-5	6·6	131, 136, 139	67	1·5	1·1
32483-12	6·4	110, 112, 117	67	1·5	1·0

The central tooth is very small, Λ-shaped and although difficult to observe clearly it appears to have five small cusps. The 1st few lateral teeth have about 7 large cusps which increase to about 10 at the 10th tooth and maintain this number to the margin. Alternating small cusps are absent.

Remarks: This subspecies bears much the same relation to *Physa jennessi skinneri* as does *P. johnsoni* to *P. gyrina*. There is as yet no evidence to indicate gene flow between *P. johnsoni* and *P. gyrina* so the former is retained as a separate species. The population of *P. j. athearni* from near Rochester, Alta., while clearly belonging to that subspecies, is not as albinistic as the type population and some gene exchange with *P. jennessi skinneri* may have occurred. Six lots from Great Slave Lake (Yellowknife Bay, Pearson Point, Christie Bay, Tochatwi Bay, Gros Cap, and an unspecified locality) collected by J. G. Oughton between 1944 and 1946 are also wholly or partially albinistic. They do not clearly exhibit the other characters of *P. j. athearni* and they are therefore assigned to *P. j. skinneri*, but their presence provides additional evidence of gene exchange between *P. j. athearni* and *P. j. skinneri*. *P. j. athearni* is therefore accorded subspecific status.

Both *Physa jennessi athearni* and *P. johnsoni* are strongly differentiated from *P. jennessi skinneri* and *P. gyrina*, however, and both occur in isolated lakes in the Rocky Mountains, a region well-known for harbouring local, endemic taxa in many phyla.

Physa jennessi skinneri Taylor
Plate 24, Figs. 1, 2; Map 69.

Physa elliptica minor Crandall, 1901: *Nautilus*, *15*: 55 (non *Physa fontinalis minor* Moquin-Tandon, 1885: 451, 452). Type locality: "Grand Rapids, Mich."

Physa skinneri Taylor, 1953: *Occ. Pap. Mus. Zool., Univ. Mich.*, No. 557: 9. Type locality: "Pleistocene, probably Illinoian age, Berends fauna. SE cor. sec. 6, T. 5N, R. 28E. Beaver Co., Oklahoma."

Diagnosis: Shell up to ½ inch tall and with an obtusely rounded apex. Juvenile of narrow ovoid form. Adult with disproportionately dominant, laterally-flattened body whorl and short, "pulled-up" spire.

Description of Juvenile: "Shell small, narrowly ovoid, polished; apex obtusely rounded. Whorls about 3, gently and regularly convex, slowly enlarging, at first overlapping; body whorl over ¾ of total shell length. Suture weakly impressed, slightly descending at first but later more strongly; above periphery of 1st whorl, at periphery of later whorls. Aperture narrowly elongate; outer lip slightly convex, more strongly so toward base; base strongly rounded; inner lip nearly straight or with a pronounced angle at junction of colu-

mella and parietal lip; peristome usually heavily callused in larger specimens, in which case the suture descends slightly at the callus; parietal wall covered by a thin callus. Nucleus smooth; later sculpture of very fine, indistinct growth lines occasionally cut by very faint, short segments of spiral striae between which growth lines may be locally more prominent." (Taylor, 1954: 9).

Description of Adult: Shell up to 12 mm long and with about 5 whorls. Body whorl dominant, disproportionately enlarged, shouldered above, flattened laterally, rather sharply rounded below, and comprising about 5/6 of the total shell length. Spire appearing peculiarly pinched and pulled-up, with the penultimate whorl or the next preceeding whorl or both markedly attenuated or, more accurately, much less enveloped by the succeeding whorl than are the earlier whorls and therefore more exposed. Outer lip broadly curved laterally and characteristically arched centrally when viewed from the palatal side. Aperture subaurate and mainly basal. Collabral and spiral striae and growth rests well marked. Other characters are as in the juvenile.

Measurements:

Whorls	Length, mm	Width, mm	W/L	Ap L	Ap L/L
Waskasoo Creek, 3 mi S of Penhold, Alta.					
5·3	12·2	6·4	0·52	9·2	0·75
5·0	12·0	6·6	0·55	8·8	0·73
4·5	7·4	3·7	0·50	5·2	0·70
4·3	7·3	3·8	0·52	5·2	0·71
4·3	7·0	3·7	0·53	4·9	0·70
4·3	6·8	3·7	0·53	4·3	0·63
4·0	6·1	3·4	0·56	4·4	0·72
3·8	6·1	3·5	0·57	4·7	0·77
3·7	5·4	3·0	0·55	3·5	0·65
3·5	4·4	2·5	0·56	3·3	0·75
3·5	4·3	2·5	0·58	3·0	0·69
3·4	4·6	2·4	0·52	3·4	0·74

Feature	N	Range	Mean	$S.E._M$	S.D.
Waskasoo Creek, 3 mi S of Penhold, Alta.					
L, mm	12	4·3 —12·2	6·97	—	—
W/L	12	0·50— 0·58	0·542	0·007	0·024
Ap L/L	12	0·63— 0·77	0·712	0·012	0·041
Whorls	12	3·4 — 5·3	4·13	—	—

Feature	N	Range	Mean	$S.E._M$	S.D.
Small Pond, Ernfold, Sask. (adults)					
L, mm	14	8·8 —11·5	10·16	—	—
W/L	14	0·49— 0·59	0·534	0·007	0·024
Ap L/L	14	0·68— 0·78	0·731	0·007	0·025
Whorls	14	4·5 — 5·3	4·94	—	—
Lydia Lake, 23 mi E of Longlac, Ont. (juveniles).					
L, mm	22	2·7 — 4·1	3·53	—	—
W/L	22	0·50— 0·59	0·550	0·004	0·019
Ap L/L	22	0·61— 0·72	0·682	0·006	0·027
Whorls	22	2·9 — 3·6	3·43	—	—

Records:

In addition to the 20 published records, there are over 100 collections of this subspecies now available from the research area. All are shown on Map 69 and are too numerous to list. Only peripheral localities are given below.

Moose River system. Smoky Falls, Kapuskasing, Ont. (Miller, 1966: 239). Shipsands Island, Moose River estuary, Ont. (1953, J. L. Chamberlin!).

Albany River system. Lydia Lake, 23 mi E of Longlac, Ont. Klotz Lake, west end, 30 mi E of Longlac (4 collections). Pools on bank of Albany River, also small brook, both near Fort Albany, Ont. (all this survey).

Attawapiskat River system. Lake Attawapiskat Ont. (Hibbard & Taylor, 1960: 119). Attawapiskat River, 17 mi and 20 mi W of Attawapiskat, Ont. Muskeg 1 mi E of Attawapiskat (all this survey).

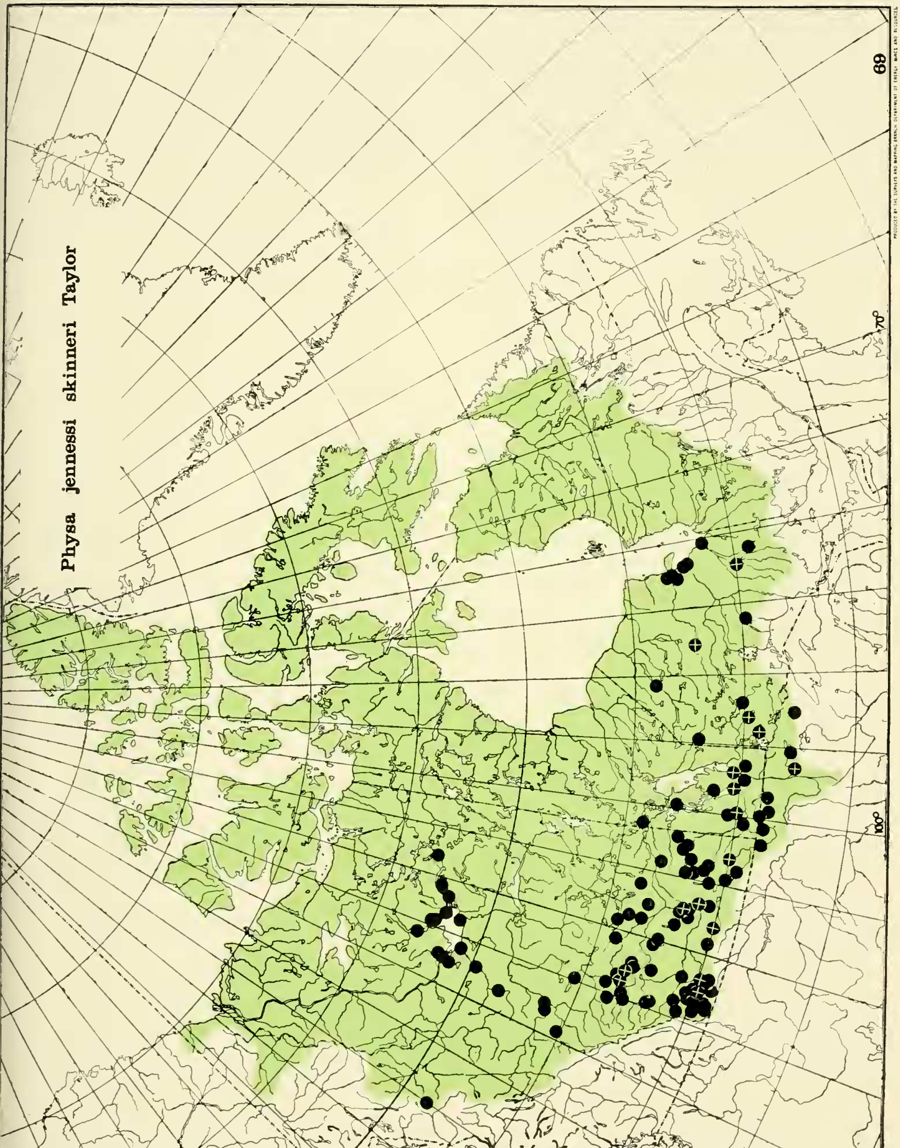
Severn River system. Severn Lake, cove at island in south end of lake, Ont. (54°00′N, 90°40′W) (this survey).

Nelson River drainage area (Winnipeg River, Red River, Lakes Manitoba-Winnipegosis, Saskatchewan River and Nelson River systems) and associated inland drainage areas. Common throughout the whole region west of the Precambrian Shield. Only a few localities on the Shield are known, viz.: Pelican Lake, Sioux Lookout, Ont. (this survey). Wabigoon, Ont. 8 mi S of Finland, Ont. 2 mi N of Reed Narrows, Lake of the Woods, Ont. (all Hibbard & Taylor, 1960: 119). Outlet of Stout Lake Ont. (52°08′N, 94°44′W) (this survey).

Churchill River system. 2 mi NE of Bonnyville, Alta. ½ mi S of Goodsoil, Sask. 3 mi NW of Meadow Lake, Sask. (all 1962, F. R. Cook & C. B. Powell!).

Mackenzie River system. Leith River [Little Burnt River], 2 mi NNW of Whitelaw, Alta. Cardinal Lake, 8½ mi WNW of Grimshaw, Alta. Lesser Slave Lake, Slave Lake, Alta. Tawatinaw River, 1 mi N of Rochester, Alta. (all this survey). Dease Lake, B C. (1962, S. D. MacDonald!). 30 mi W of Rae Junction, N.W.T. (1965, R. Hartland-Rowe!). Hay River, Hay River Township, N.W.T. Mackenzie River, Dory Point, near Hwy. No. 3, N.W.T. Mackenzie River at ferry crossing west of Great Slave Lake. Great Slave Lake at Frank Channel and at Latham Island. Yellowknife River, 7 mi N of Yellowknife (all 1966, R. W. Coleman!). Great Slave Lake, numerous localities (1944–46, J. G. Oughton!). Kakisa Lake N.W.T. (date? W. Kennedy!).

Distribution: Southern Canada and northern United States from eastern Ontario and James Bay (south of 55°N) west to Alberta, British Columbia and southern Northwest Territories (vicinity of Great Slave Lake) and southwest to Utah. See Map 69. The records for Fort Severn, Ontario (Hibbard & Taylor



Physa jennessi skinneri Taylor

1960: 119) and upper Yukon River drainage in Alaska (Miller, 1966:238) probably represent *P. j. jennessi.*

Biology and Ecology: The 53 lots of *Physa jennessi skinneri* collected during this survey are from the following habitats: 13 are from large lakes, 4 from small lakes, 7 from ponds (some of which may dry out in late summer), 3 from rivers 50 to 100 feet wide, 10 from rivers 25 to 50 feet wide, 11 from streams 10 to 25 feet wide, 2 from streams 5 to 10 feet wide, 2 from marshes, and 1 from muskeg. Vegetation was abundant at most habitats, moderately abundant at some, and sparse at a few. Bottom deposits were partly or entirely of mud in 50 localities, of sand only at 2, and of rock only at 1. Current was slow or not perceptible at all lotic habitats.

Numerous collections were also made in Alberta during the summer of 1965 and 1966 by Dr. R. Hartland-Rowe of the University of Alberta at Calgary. Many of these habitats appear to be vernal.

According to Miller (1966: 239) " the Recent records of this [subspecies] suggest that it lives in shallow bodies of water, either perennial or temporary, ponds, sloughs, or backwaters along streams. " A collection from the Bay of Quinte, Lake Ontario, is also cited.

The present data indicate that a wide variety of habitats is suitable especially shallow, eutrophic areas with an abundance of vegetation and a muddy substrate. These may be either vernal or perennial. The presence of *Physa jennessi skinneri* at a depth of 15 feet in Klotz Lake on June 2, 1965 indicates that seasonal migration may also occur. Klotz Lake appeared to be homeothermous on that date and summer thermal stratification had not begun.

The soft parts and radula of *Physa jennessi skinneri* have not been previously described. In some populations the foot is narrow and whitish-tan, the head and tentacles are grey, and the mantle as seen through the pale shell has whitish, circular spots on a pale grey background. Variation in colouring occurs, however, and some specimens are more heavily pigmented throughout with small grey-brown mantle spots on a black background, while others are less pigmented and are almost albino. Young specimens appear to be somewhat less heavily pigmented than adults. The mantle digitations are very conspicuous on some specimens, especially juveniles, and may then extend well beyond the parietal wall. Mantle digitations, when visible, number approximately 4 to 6 on the columella and 3 to 4 on the parietal wall.

The radulae of specimens from Ernfold, Sask. (NMC 29305), Millarville, Alta. (NMC 39860), Lindbrook, Alta. (NMC 29311), and Severn Lake, Ont. (NMC 29312) were extracted and examined, with the following results:

Specimen No.	Shell Length mm	Lateral Teeth (One side, one row)	No. of Rows	Radula Length mm	Radula Width mm
29305–A	11·3	115	71	2·2	1·7
39860–A	9·1	122	65	1·7	1·2
29311–B	4·6	96	58	1·2	1·0
29312–A	3·4	95	56	1·2	1·0

The central tooth of the 2 larger specimens has 7 cusps and in the 2 smaller specimens it appeared to have 5 cusps. The apices of these cusps align to form an obtuse inverted v, i.e. ∧. The larger specimens have 6 cusps on the 1st laterals which increase to 8 by the 5th or 6th lateral and continue to the margin. No small intermediary cusps were seen. In the smaller specimens the details of individual teeth were difficult to observe at 1000x but the lateral teeth appeared to bear some tiny, intermediary cusps between the large cusps.

Remarks: Although the body whorl is roundly shouldered and laterally flattened while earlier whorls are more evenly curved, the ratios W/L and ApL/L do not appear to change significantly with growth (see " Measurements ").

The presence of an elevated penultimate or first pre-penultimate whorl or both in *Physa jennessi skinneri* is almost always a reliable character for the differentiation of that subspecies from *P. j. jennessi*. A few lots from the vicinity of James Bay and southwestern Hudson Bay are difficult to place with certainty, however. They have been assigned to the subspecies they most closely resemble, but the existence of gene flow between the 2 taxa is strongly suggested. It is for this reason that subspecific relationships have been proposed here.

Conchologically there are many striking similarities between *Physa jennessi* (*s. lato*) and *Physa fontinalis* (L) of Europe. At least 1 competent malacologist (O. Boettger, 1880) has confused the 2 species. As pointed out by Taylor (1960: 64): " When anatomical data are available on the American species, it may be possible to evaluate... shell characters, and perhaps even to recognize subgenera of *Physa*. "

Physa gyrina Say

Plate 13, Fig. 1; Pl. 24, Figs. 7-9; Map 70.

Physa gyrina Say, 1821: *J. Acad. natr. Sci. Philad.*, *2*: 171 (Binney reprint, 1858: 67). Type locality: " Bowyer Creek, near Council Bluff [Council Bluffs, Iowa]."

Physa Hildrethiana Lea, 1841: *Proc. Amer. phil. Soc.*, *2*: 32. Type locality: " A lake in Illinois."

Physa gouldi Clench, 1935: *Nautilus*, *49*(1): 30-32, pl. 7: 5 (*Nautilus*, *48*). Type locality: " Mouse River 6 mi N of Towner, McHenry Co., North Dakota."

Diagnosis: Shell up to about 1 inch tall (but ordinarily much less); variable; thin to slightly thickened; whorls about 5, inflated; apex acute and reddish and with spiral lines visible in most specimens.

Description: Shell up to about 24 mm long, sinistral, variable, of moderate relative elongation, thin to slightly thickened, transparent to sub-opaque, narrowly umbilicate or non-umbilicate, pale yellowish-brown to greyish-brown, with a short spire and a dull surface. Nuclear whorl small, rounded, finely punctate and generally red to reddish-brown. Whorls gently rounded, each partly enveloping the preceding whorl and numbering 5 to 6. Spire acute, rather short and comprising about $\frac{1}{8}$ of the shell length. Sutures impressed and bordered below by a narrow, pale band. Body whorl large and well-rounded but not inflated. Aperture " loop-shaped ", mainly basal, acute above, flatly rounded laterally, rounded basally, and occupying about 6/10 to 8/10 of the shell length. Outer lip thin to slightly thickened and bordered inside by a prominent red or reddish collabral band. Columella oblique, thin to slightly thickened, and with a thin to moderately thick and extensive wash of callus on the parietal wall. In some specimens the lower part of the inner lip is raised, exposing a narrow umbili-

PLATE 24. Physidae

FIG. 1. *Physa jennessi skinneri* (juv.), Lydia Lake, near Longlac, Ontario (NMC 19336, 3·9 mm) . . . . , ... p 368.

FIG. 2. *Physa jennessi skinneri*, Near Millarville, Alberta (NMC 39861, 8·2 mm) . . . . , . p 368.

FIG. 3. *Physa jennessi* (paratype), near Bernard Harbour, Northwest Territories (NMC 46251, 8·4 mm) . . . . p 362.

FIGS. 4, 5. *Physa jennessi athearni* (holotype), Horseshoe Lake about 10 mi SE of Jasper, Alberta (NMC 46384, 6·3 mm) . . . . p 365.

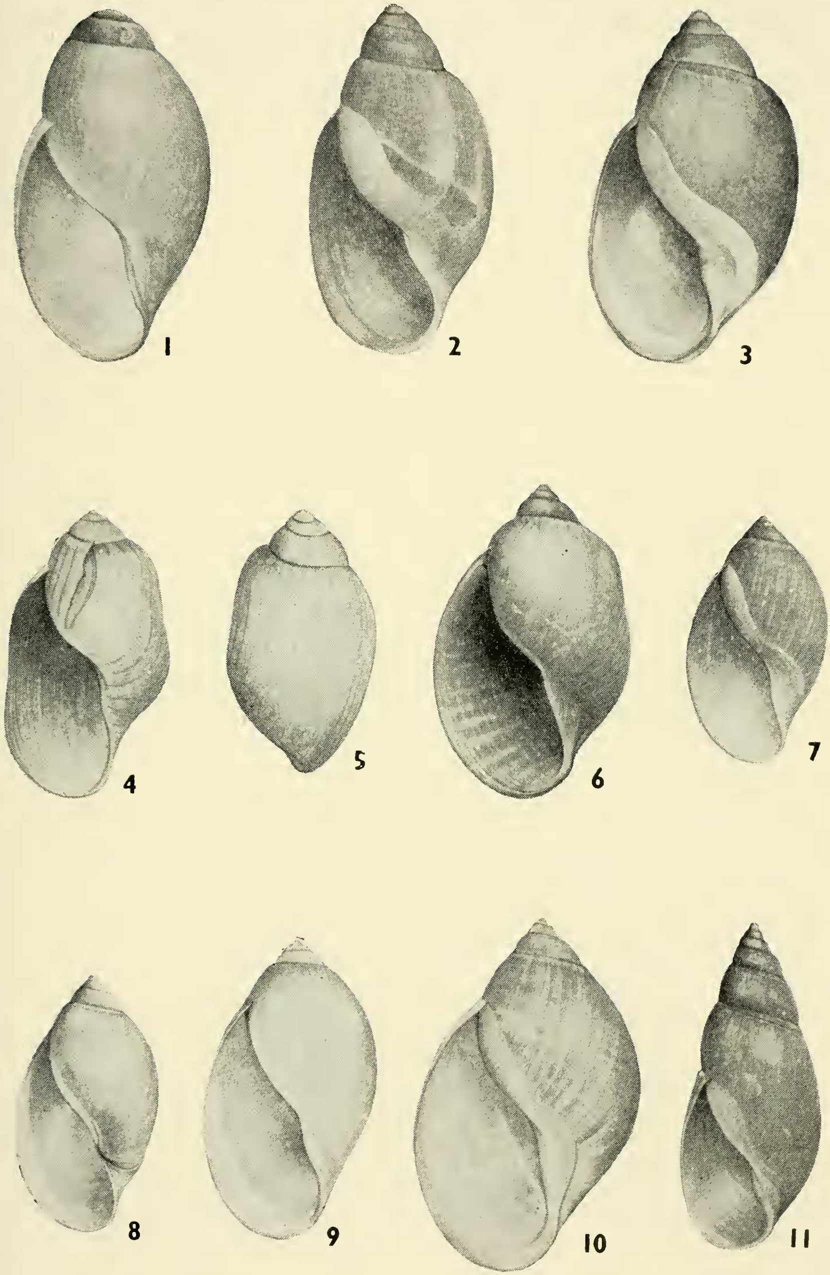
FIG. 6. *Physa jennessi athearni* (paratype) Horseshoe Lake about 10 mi SE of Jasper, Alberta (NMC 32483, 7·5 mm) . . . . p 365.

FIG. 7. *Physa gyrina*, Lac de Montigny, near Val d'Or, Quebec (NMC 19046, 11·7 mm) . . . . p 373.

FIGS. 8, 9. *Physa gyrina*, Macamic Lake, near La Sarre, Quebec (NMC 19420, 12·1 and 13·9 mm) . . . . p 373.

FIG. 10. *Physa johnsoni*, outlet of Middle Spring, Banff, Alberta (NMC 40517, 8·4 mm) . . . . p 381.

FIG. 11. *Aplexa hypnorum*, 6 mi W of Star City, Saskatchewan (NMC 39940, 15·5 mm). . . . . . . p 383.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cus. Sculpture consists of numerous coarse lines of growth, in some specimens also of 1 or more internal varices visible externally as whitish collabral bands, and in many populations also of crowded, impressed spiral lines crossing the growth lines. These spiral lines may be strong and conspicuous, moderately strong, faint, or absent.

Measurements:*

Whorls	N	Length, mm	W/L	ApL/L
Lillabelle Lake, 5 mi N of Cochrane, Ont. (July, 31, 1960).				
5·0—5·4	7	9·9–(12·7)–14·4	0·51–(0·576)–0·65	0·72–(0·749)–0·82
4·5—4·9	19	8·2–(10·3)–12·7	0·50–(0·543)–0·60	0·69–(0·730)–0·78
4·0—4·4	13	6·5–(7·79)– 9·3	0·52–(0·569)–0·61	0·70–(0·759)–0·83
3·5—3·9	4	5·3–(6·20)– 6·7	0·54–(0·555)–0·57	0·68–(0·722)–0·75
3·0—3·4	2	3·2–(3·30)– 3·4	0·59	0·72–(0·735)–0·75
2·5—2·9	1	1·9	0·68	0·74
Assiniboine River, Winnipeg, Man. (Aug. 17, 1961).				
5·5—5·6	3	16·1–(17·2)–17·8	0·54–(0·556)–0·57	0·68–(0·686)–0·70
5·0—5·4	3	14·2–(14·3)–14·4	0·54–(0·578)–0·60	0·70–(0·715)–0·73
4·7—4·9	4	9·8–(10·8)–11·2	0·62–(0·632)–0·64	0·65–(0·704)–0·73

* Comparative measurements of size groups are shown. The largest specimen seen is from a brook 6 mi S of Cochrane, Ont., collected July 23, 1961 (cited under "Remarks"). Its measurements are: whorls =5·6, length=24·1 mm, W/L=0·644, ApL/L=0·809.

Records:

Some 350 lots of *Physa gyrina* from the research area, collected during this survey and acquired from other sources, have been examined. The localities have been plotted on Map 70 and are far too numerous for listing. Only marginal records are given below.

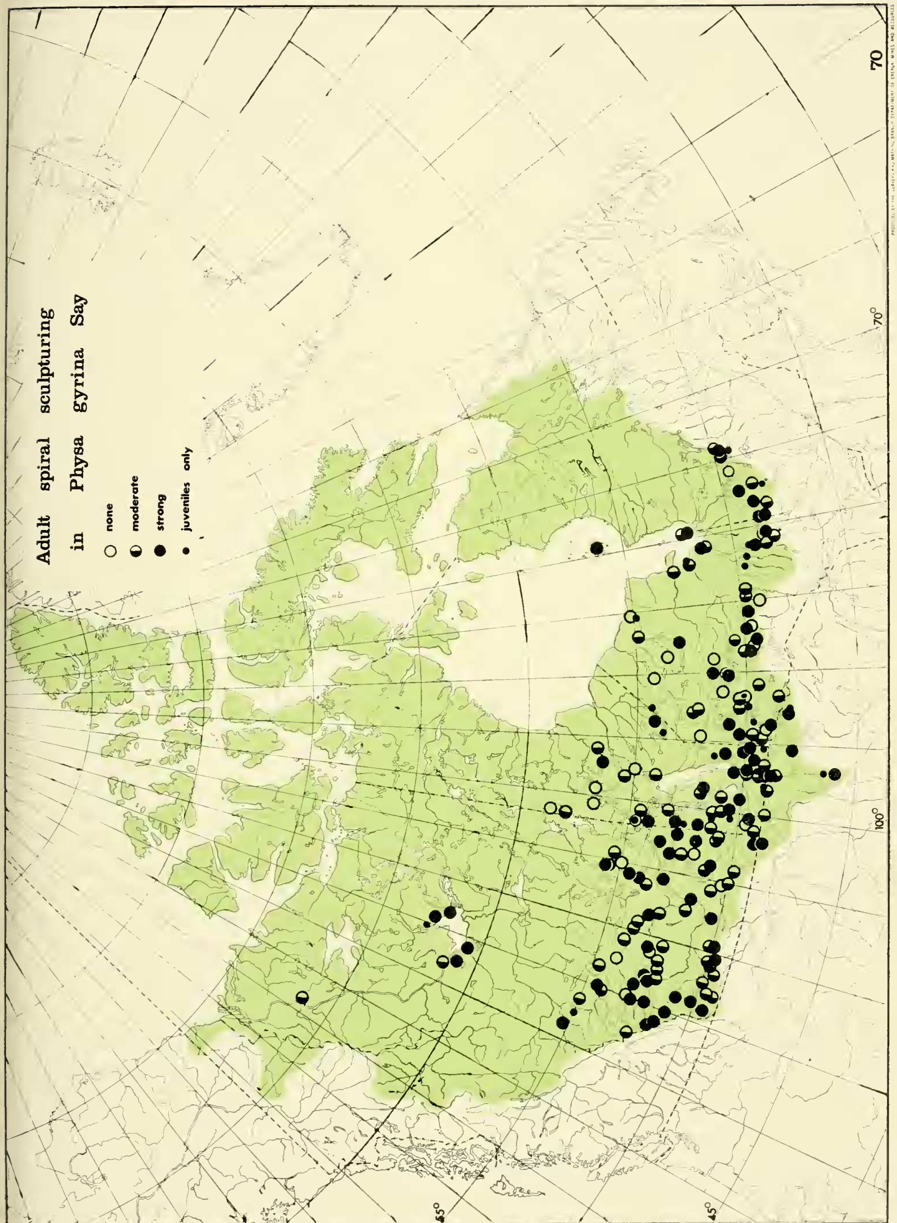
Eastern Hudson Bay and James Bay drainage areas. Bloody Island Camp, Belcher Islands (1958, Fish. Res. Bd.!). Charlton Island, James Bay (4 localities: 1920, F. Johansen!; 1933, H. G. Richards!).

Nottaway River system. Small lake 18 mi S of Chibougamau, Que. Chibougamau River, 13 mi S of Chibougamau. Lac Doré, 10 mi SW of Chibougamau. Outlet of Lac Pascalis, 13 mi S of Senneterre, Que. Bell River, Senneterre. Lac Parent, 5 mi N of Senneterre. Bell River, 33 mi N of Senneterre (all this survey).

Harricanaw, Moose, Albany, and Attawapiskat River systems. Common wherever collections were made from headwater localities to the vicinity of James Bay.

Winisk, Shell Brook, Severn, and Hayes River, systems. Winisk River drainage area: Shibogama Lake, west end (53°31′N, 88°35′W). Vicinity of Winisk (4 localities) (all this survey). Shell Brook drainage area: lake, source of Shell Brook, at narrows (55°20′N, 87°17′W) (this survey). Severn River drainage area: Severn Lake, north end (54°05′N, 90°42′W). MacDowell Lake (52°14′N, 92°47′W). North Spirit Lake, at outlet (52°21′N, 93°02′W). Deer Lake, near Deer Lake (village) (52°09′N, 94°00′W) (all this survey). Hayes River drainage area: Stull Lake, at outlet, Ont. (54°29′N, 92°34′W). Red Sucker Lake, W end, Man. (54°10′N, 93°57′W) (both this survey).

Nelson River system (all drainage areas). Widespread and abundant throughout the region from western Ontario to western Alberta and from Lake Traverse, Minnesota north at least to Thicket Portage, Wintering Lake, Man.


Adult spiral sculpturing
in Physa gyrina Say
none
moderate
strong
juveniles only
70
70°
100°
45°
45°

(55°19′N, 97°42′W) (this survey and other sources).

Churchill River system. Montreal Lake—Lac la Ronge region, Sask. (several localities). Reindeer Lake, Brochet, Man. Eden Lake, at outlet, Man. (56°38′N, 100°15′W). Opachuanau Lake, Man. (56°44′N, 99°37′W). White Stone Lake, Man. (56°27′N, 97°30′W) (all this survey).

Mackenzie River system. Lake Annette, Jasper National Park, Alta. (1964, R. W. Coleman!). ¾ mi N of Little Smoky, Alta. (1965, R. Hartland-Rowe!). Clairmont Lake, 2 mi NE of Clairmont, Alta. Inlet of Horn Lake, 10 mi SW of Whitecourt, Alta. Baptiset Lake, 12 mi W of Athabasca, Alta. (all this survey). Mouth of Hay River, N.W.T. (1917, E. M. Kindle and E. J. Whittaker!). Great Slave Lake and vicinity, several localities (1944–46, J. G. Oughton!). Mills Lake, N.W.T. (1917, E. M. Kindle!) Fossil Lake, N.W.T. (66°17′N, 128°55′W) (1962, E. W. Innes!). Lakes about 30 mi S of Aklavik, N.W.T. (1940, K. H. Lang!).

Distribution: Canadian Interior Basin from Belcher Islands and southeast of James Bay westward and northwestward (south of tree-line) to the Mackenzie River Delta; Great Lakes–St. Lawrence drainage area; Mississippi-Missouri drainage area and (Baker, 1928a: 452) Gulf of Mexico drainage area from Alabama to Texas.

Biology and Ecology: *Physa gyrina* occurred in all sizes of perennial water habitats and in many temporary overflow swamps and pools which are marginal to permanent streams and lakes. In the research area it was never collected in isolated vernal ponds. This is in contrast to statements by Baker (1928a: 454), Taylor (1960: 63), and DeWitt (1955: 40, etc.) that *P. gyrina* (*s. str.*) and *P. gyrina* form *hildrethiana* (not differentiated from *P. gyrina* (*s. str.*) in the present work, see " Remarks ") are characteristic of swales, summer-dry ponds, and drainage ditches, as well as perennial-water habitats. *P. gyrina* may occur in vernal habitats in the southern part of the Canadian Interior Basin but it apparently does not occur in such habitats in the central and northern parts of the research area. Probably it cannot survive the colder northern winters when not covered by unfrozen water.

Submersed aquatic vascular plants were present at nearly all localities where *Physa gyrina* was collected, substrates were various but most commonly of mud, and current was slow at most lotic localities.

Physa gyrina is very active and moves rapidly with an even, gliding motion. Specimens from Sturgeon River, near Superior Junction, Ont. were seen to shake their shell vigorously from side to side when another snail crawled over it.

Baker (1928a: 450) has described the radula and anatomy of the species. The radula formulae given vary from 95-1-95 to 120-1-120. Specimens from Sand Lake, 8 mi N of Virginia, Minn. and from Two Rivers, Hallock, Minn. have tooth counts within these limits, but specimens from Murray Lake 4 mi S of Seven Persons, Alta. have about 150 lateral teeth on each side of the central tooth. One of these specimens, 19·0 mm long, has a radula 3·36 mm long and 2·52 mm wide with 84 rows of teeth and about 152 teeth on 1 side of the central tooth, counted near the middle of the radula. Wurtz (1949b) found that radular characters in *Physa heterostropha*, a species from eastern North America, varied widely. His conclusion, that radular characters were not useful for differentiating species of *Physa* in eastern Pennsylvania, is probably applicable to the subarctic region as well.

The ecology, reproduction, fecundity, and growth of *Physa gyrina* have been described in a series of papers by DeWitt (1954a, b, c; 1955). In natural populations in Michigan living in perennial water habitats the life span was normally 12 to 13 months whereas those

living in vernal habitats spent many months in aestivation and survived for a much longer period. The main period of oviposition occurred when water temperatures reached 10°-12°C in the spring. Some oviposition was also observed in the fall. Russell-Hunter (1964: 100) has reviewed earlier work which shows that different reproductive patterns (i.e., 1 or 2 broods a year with or without replacement) may occur in separate populations of the European *P. fontinalis*. This may be the case with *P. gyrina* as well.

Remarks on Growth: The measurements given above indicate that in the research area and within the size range attained by specimens with about $3\frac{1}{2}$-$5\frac{1}{2}$ whorls, there is little change in relative dimensions with growth. This is not in agreement with DeWitt (1954a: 133) who reared specimens from a Michigan population in the laboratory. Unusually small or large specimens do diverge in relative dimensions, however.

An effort was made to determine whether maximum size in *Physa gyrina* could be correlated with habitat. The length of the largest specimen was measured in each of the 211 lots collected during this survey. Only 6 lots had specimens exceeding 20 mm in length and all 6 came from stream habitats. The largest specimen, 24·1 mm long, was collected from a small brook 6 mi S of Cochrane, Ont. on July 23, 1961. The 2nd largest, about 23 mm long (spire tip broken), was collected on June 12, 1965 in Nanton Creek, Nanton, Alta, a slow-moving stream about 30 feet wide. At each of these localities a single, large *Physa* was the only mollusc found. The other 4 lots containing unusually large specimens (21 or 22 mm long) were all collected in prairie creeks and rivers between June 10 and July 13, 1965. None were single specimens, however.

The 6 streams were much alike in current (moderate to slow), in vegetational density (medium to sparse) and in apparent water purity (i.e., unpolluted) but were quite unlike in width (less than 10 feet to over 100 feet) and bottom sediments (mud, sand, gravel, rocks). The other 205 lots were from many kinds of habitats and no correlations with size were evident.

The field study which forms the basis for this work covered 9 field seasons and about 600 collecting stations. It is unquestionably significant, I think, that (*a*) on only 2 occasions was a single *Physa* the only mollusc found after a thorough search at a collecting station and (*b*) that these 2 stations produced the 2 largest *Physa* specimens known from the Canadian Interior Basin. (Several stations produced only 1 *Physa*, but other molluscs were also present and the size of the *Physa* was, in each case, quite unexceptional.) The fact that the 6 largest specimens are all from stream habitats is probably also significant.

Several authors (see Russell-Hunter, 1964: 101) have shown that some species of pulmonates show reduction in growth rates, in maximum size, and in fecundity when reared in dense cultures. It appears likely to me that this phenomenon may have survival value for the species. Numerous, small individuals (resulting from the effects of crowding) would be more likely to be accidentally transported by birds to new habitats than would fewer, large individuals, and populations which were in danger of extinction through overcrowding might therefore be more likely to found populations elsewhere.

Numerous observations and experiments reported in the literature have shown that some species may attain unusually large size when reared with only a few members of the same species

or when occurring naturally in certain large water bodies. The present data suggest that at least in *Physa gyrina* an interspecific effect also may exist and that the absence of other species of molluscs may also contribute to the attainment of unusually large maximum size. If this is true then the need for research on such interspecific effects is evident. Mutual inhibition of growth may prove to be another method of assessing taxonomic relationship.

Remarks on Variation: Strength and frequency of spiral sculpture has often been used in differentiating *Physa gyrina* "*hildrethiana*" from *P. gyrina* (*s. str.*). Sculpturing also appears to be reasonably constant within populations. In order to test the validity of taxonomic distinctions based on sculpturing, all available lots containing specimens 8 mm long or more were classed for spiral sculpturing using the code: 1, none; 2, moderate (visible but not obvious) and 3, strong (immediately obvious). The values derived from application of this code were plotted on Map 70.

The results indicate that sculpturing varies widely and randomly between populations. Unsculptured, moderately-sculptured, and strongly-sculptured lots occur throughout the whole region. Strength of sculpturing is therefore not a useful criterion for distinguishing subspecies of *Physa gyrina* in the research area. There is also no evidence that the distribution of the strongly sculptured morph "*hildrethiana*" is elsewhere related to geography and since all intergrades exist that taxon is here reduced to synonymy.

All these lots were also classed for average values of the ratio aperture length to length (ApL/L) shown by specimens 8 mm long or longer. Results varied from approximately 0·6 to 0·8 and were distributed in a random manner. Therefore that character is also considered not useful in distinguishing subspecies in *Physa gyrina*.

Other shell characters that show variation are (1) presence or absence of varices, (2) relative thickness of shell or of columella, (3) presence or absence of a reddish collabral band at the inner edge of the outer lip, (4) presence or absence of a red or reddish apex, (5) relative convexity of whorls, and (6) relative pigmentation of the shells. Characters (1) and (2) appeared to show some positive correlation with water hardness but no correlation with geography. Character (6) is of interest in that populations with pale-coloured shells are frequent in the Attawapiskat and Winisk River systems. This phenomenon is seen in other species from that region as well (e.g., in *Lymnaea exigua*) and it is not considered taxonomically significant.

Externally visible characters of the soft parts that show intrapopulation variation are (1) relative albinism and melanism, (2) relative size and conspicuousness of mantle spots, and (3) the shape, size, and number of mantle digitations. All these characters varied, apparently randomly, but the extent of their variation was not analyzed in detail.

It is virtually certain that all citations of *Physa ancillaria* Say and of *P. heterostropha* Say from the region under consideration are based on *P. gyrina*. *P. gouldi* Clench appears to be synonymous with *P. gyrina*. *P. integra* (Haldeman) has shell characters that would suggest that it is a hard-water ecophenotype of *P. gyrina*, but the morphology of the penial complex indicates that it is distinct, as pointed out by Baker (1928a: 461) and Wurtz (1949b: 24). *P. vinosa* Gould, from Michipicoten, Lake Superior, appears to be a separate taxon, although it may be only a subspecies of *P. gyrina*. No

specimens referable to *P. vinosa* have been seen from the Hudson Bay drainage area near Lake Superior.

Physa johnsoni Clench
Plate 24, Fig. 10; Map 68.

Physa johnsoni Clench, 1926: *Occ. Pap. Mus. Zool., Univ. Mich.*, No. 168: 2. Type locality: "middle spring, Hot Sulphur Springs, Banff, Alberta."

Diagnosis: Shell up to $\frac{1}{3}$ inch tall; highly variable; apex rather sharp; spire short but acute; body whorl dominant, inflated and evenly rounded; surface with numerous, evenly spaced lines of growth and, on abraded specimens, with white, spiral lines.

Description: Shell sinistral, small, globose, thin. Color dark reddish horn, sometimes faintly striated. Whorls $4\frac{1}{2}$ to 5, convex and well rounded, nuclear whorl darker in color. Spire rather short, terminating in an acute apex. Aperture well rounded, flaring slightly at base. Palatal lip very thin, rarely labiate. Parietal lip a thin deposit only on body whorl. Columella rather narrow, not twisted, inclined toward the left and not abruptly terminating at the body whorl but gradually continuing the general contour. Suture very well impressed, slightly indented. Sculpture of very fine growth lines but no cross striae. The loss of the periostracum on some of the most prominent growth lines gives it the appearance of striations as noted above. Varicose bands rare and most noticeable when seen from within the aperture.

Measurements:

Middle Spring outlet, 0·8 mi E of Middle Spring, Banff, Alta. (this survey).

Whorls	N	Length, mm	W/L	Ap L/L
4·7—4·8	5	7·7–(8·4)–8·8	0·56–(0·58)–0·60	0·63–(0·66)–0·70
4·5—4·6	9	7·0–(7·3)–7·6	0·53–(0·55)–0·57	0·63–(0·67)–0·70
4·3—4·4	9	6·3–(6·7)–7·0	0·52–(0·55)–0·59	0·63–(0·67)–0·71
4·1—4·2	3	5·8–(6·6)–7·3	0·55–(0·56)–0·58	0·67–(0·68)–0·70
3·9—4·0	5	4·7–(5·0)–5·4	0·53–(0·55)–0·59	0·61–(0·66)–0·71
3·7—3·8	4	4·7–(4·9)–5·0	0·58–(0·58)–0·60	0·68–(0·69)–0·72
3·5—3·6	0	—	—	—
3·3—3·4	1	4·5	0·60	0·71

Middle Spring, Hot Sulphur Springs, Banff, Alta.* (Clench, 1926: 3).

Feature	N	Range	Mean	$S.E._M$	S.D.
Length (L), mm	6	5·5 —7·5	6·17	—	—
Width (W), mm	6	3·8 —5·2	3·33	—	—
W/L	6	0·65—0·69	0·677	0·007	0·017
Ap L/L	6	0·67—0·80	0·737	0·026	0·056
Ap W/Ap L	6	0·42—0·48	0·447	0·009	0·022

* The measurements of 1 specimen not included above, appear anomalous, viz.: L=6·5, W=5·5, Ap L=5·3, Ap W=2·5.

Feature	N	Range	Mean	$S.E._M$	S.D.
Middle Spring outlet, 0·8 mi E of Middle Spring, Banff, Alta.					
Length (L), mm	36	4·5 —8·8	6·58	—	—
Width (W), mm	36	2·7 —5·1	3·69	—	—
W/L	36	0·52—0·60	0·563	0·007	0·023
Ap L/L	36	0·61—0·71	0·673	0·004	0·025
Spiral striae **	36	1·0 —3·0	2·19	0·09	0·51
Whorl convexity **	36	1·5 —3·0	2·18	0·09	0·51
Whorls	36	3·4 —4·8	4·29	—	—

** Code values are: spiral striae: 1, absent; 2, present but weak; 3, strong; whorl convexity: 1, spire whorls flat; 2, flatly rounded; 3, rounded.

Records:

Saskatchewan River system. Upper Hot Springs, Banff, Alta. (1927, T. Ulke!). Middle Spring, Hot Sulphur Springs, Banff, Alta. (type lot). Outlet of Middle Spring, 0·8 mi E of Middle Spring (i.e., 300 yds S of Banff Springs Hotel), Banff (July 23, 1965, H. D. Athearn, this survey). Kidney Spring, Hot Sulphur Springs; Cave and Basin; and Cold Spring, Vermilion Lake, Banff (all Jan. 1927 and Jan. 1929, O. Bryant!).

Distribution: Hot and cold springs and their effluent streams, Banff National Park, Banff, Alberta.

Biology and Ecology: The water temperature at the type locality was 92°F, according to original data cited by Clench. Water temperature in Middle Spring outlet near the Banff Springs Hotel was reported as about 75°F. The presence of *Physa johnsoni* in a cold spring (see " Records ") indicates that high temperature is not vital for the species, however.

The outlet stream of Middle Spring where visited was about 5 feet wide and 2 inches deep, with a rapid current and clear water, a rocky bottom, and with moss and algae growing on the rocks. *Lymnaea proxima* Lea occurred there in the same habitat with *Physa johnsoni* and in approximately equal numbers. The *L. proxima* were all small, about the same size as the *P. johnsoni*, and had the same reticulate pattern of whitish collabral and spiral lines.

Two specimens from the above locality were examined for radular characters, with the following results:

Specimen No.	Shell Length mm	Lateral Teeth (One side, one row)	No. of Rows	Radula Length mm	Radula Width mm
32244–1	7·6	105	61	1·7	1·2
32244–2	6·2	102	60	1·7	1·1

The central tooth was broad and Λ-shaped with 7 cusps. The 1st lateral tooth had 5 cusps, with cusps increasing to about 8 on the 6th lateral tooth and maintaining that number to the margin. A few additional small cusps were also seen alternating with the large cusps on some of the teeth which have 8 large cusps.

Remarks: This species appears to be related to *Physa gyrina* Say. It is morphologically divergent from that species, however, and apparently deserves specific status.

Genus *Aplexa* Fleming

Aplexa Fleming, 1820: [*in*] *Brewster's Edinburgh Encyclopedia*. 14: 617. Type species: *Bulla hypnorum* L., by monotypy. *Aplexa* Fleming has been placed on the Official List of Generic Names in Zoology (Name No. 812) by Opinion 335 of the International Commission on Zoological Nomenclature, 1955.

Shell sinistral, medium-sized, elongate, smooth, shiny, and without prominent spiral sculpture. Soft parts as in *Physa* except that the edge of the mantle is not digitate and does not extend over the shell. The eggs of *Physa* and *Aplexa* are also quite different (Bondesen, 1950).

Only a few species of *Aplexa* have been described and these may all be biological synonyms of *Aplexa hypnorum* L. (The large species of Central and South America assigned by some authors to *Aplexa* are now recognized as belonging to *Stenophysa* von Martens). *Aplexa* is circumboreal and its geologic range extends from Jurassic or Upper Cretaceous to Recent time (Zilch, 1959: 90).

Aplexa hypnorum (Linnaeus)

Plate 13, Fig. 2; Pl. 24, Fig. 11; Map 71.

Bulla hypnorum Linnaeus 1758: *Systema Natura*, 10th ed., p 727. Type locality: "in Europae *Muscis humentibus*."

Physa elongata Say, 1821: *J. Acad. natr. Sci. Philad.*, *2*: 171 (Binney reprint, 1858: 68). Type locality: "Inhabits shores of Illinois . . . very common in stagnant ponds on the banks of the Mississippi."

Diagnosis: Shell up to about $\frac{3}{4}$ inch long, sinistral, conispiral, elongated, with flatly rounded whorls, polished surface, and aperture length about half the length of the shell.

Description: Shell up to about 18 mm long, sinistral, elongated, thin, transparent, non-umbilicate, brownish (but appearing blackish when containing the soft parts), with a long spire and glossy surface. Nuclear whorl rounded, finely punctate and amber coloured. Later whorls flatly rounded, each partly enveloped by the succeeding whorl and (including the nuclear whorl) numbering 6 to 7. Spire acute, elongate, and comprising about $\frac{1}{3}$ of the shell length. Sutures impressed and bordered below by a narrow white band. Body whorl flatly rounded and subcylindrical. Aperture acute above, subtruncate below, and about half the length of the shell. Outer lip thin, flatly rounded, and only slightly thickened within. Columella oblique, narrow, slightly twisted, and with a very thin wash of callus on the parietal wall. Sculpturing consists of fine lines of growth and (principally in arctic populations) of fine spiral lines, especially where the periostracum is abraded. Periostracum polished, thin, brownish horn-coloured, and often with a greenish glint.

Measurements:

Whorls	Length mm	Width mm	W/L	Ap L	Ap L/L	Spiral * Striae	Whorl * Convexity
Small Lake, south coast, Banks I., N.W.T.							
ca. 6	6·2	2·7	0·43	3·5	0·56	2·0	2·0
5+	5·3	2·5	0·47	2·9	0·55	1·0	1·5
5+	5·5	2·7	0·50	3·1	0·56	1·0	2·0
5·3	5·3	2·3	0·44	2·9	0·55	1·5	2·0
5·2	4·6	2·4	0·53	2·7	0·58	2·0	2·5
5·0	4·2	2·1	0·50	2·5	0·60	1·5	2·0
4·8	4·1	1·9	0·47	2·5	0·61	1·5	1·5
4·5	3·6	1·9	0·53	2·2	0·63	2·0	2·0
5 mi N of Innisfail, Alta.							
7·4	17·3	7·1	0·41	8·6	0·50	1·0	2·0
7·3	17·8	7·5	0·42	10·0	0·56	2·0	2·0
7·2	16·3	6·8	0·42	8·1	0·50	2·0	2·0
7·2	17·1	6·7	0·39	8·9	0·52	2·0	1·5
7·1	17·0	6·8	0·40	9·3	0·55	1·0	2·0
7·1	15·6	6·4	0·41	8·5	0·54	1·0	1·5
7·0	16·9	7·2	0·43	9·0	0·53	2·0	2·0
7·0	16·7	6·9	0·41	8·8	0·53	3·0	2·0
6·5	16·4	7·0	0·43	9·0	0·55	2·0	1·5
6·3	12·9	5·2	0·40	6·9	0·53	2·0	2·0
6·2	14·1	6·5	0·46	8·1	0·57	3·0	2·0
6·1	13·4	5·4	0·40	7·5	0·56	2·0	1·5
Lower Fort Garry, Man.							
6·8	17·4	7·2	0·41	10·2	0·59	1·0	1·0
6·7	16·0	6·3	0·39	9·0	0·56	2·0	2·0
6·7	16·4	6·8	0·41	8·9	0·54	2·0	2·5
6·6	16·2	6·5	0·40	9·1	0·56	3·0	2·0
6·6	15·3	6·1	0·40	8·5	0·56	1·0	2·0
6·5	15·3	6·2	0·41	8·4	0·55	2·0	1·5
6·4	12·2	4·3	0·35	6·4	0·52	1·0	2·0
6·1	13·6	5·3	0·39	7·1	0·52	1·0	2·0

* Code values are as in *Physa johnsoni*, i.e.: Spiral striae: 1, absent; 2, present but weak; 3, strong; Whorl convoxity: 1, spire whorls flat; 2, flatly rounded; 3, rounded.

Records:

Moose River system. Moose River, beach at Moosonee, Ont. (this survey). Swamp, Moose Factory, Ont. (*ca.* 1950, E. A. Chamberlin!).

Albany River system. Vernal pool 20 mi W of Hearst, Ont. Lydia Lake, 23 mi E of Longlac, Ont. (both this survey). Near Fort Albany, Ont., (4 localities) (1920, F. Johansen! (1) and this survey (3)).

Attawapiskat River system. Muskeg near Attawapiskat River, 1 mi E of Attawapiskat, Ont. Woods pool, 3 mi E of Attawapiskat (both this survey).

Winisk River system. Muskeg, 6 mi E, 4 mi E, and at Winisk, Ont. (all this survey).

Hayes River system. Red Sucker Lake, Man. (54°10′N, 93°57′W) (this survey).

Winnipeg River system. Mack Lake (48°24′N, 91°00′W), Ont. (Baker, 1939b: 99). Roadside ditch 6 mi W of Whitemouth, Man. (this survey). Brereton, Man. Whiteshell River District, Man., (4 localities) (all Mozley, 1938: 113). Winnipeg River, 7 mi E of Seven Sisters Dam, Man. (1951, W. E. Godfrey!).

Brokenhead, Red, Assiniboine, Saskatchewan, and Nelson River systems; Devil's Lake, Quill Lakes, and Lakes Manitoba-Winnipegosis drainage areas. About 80 collections and literature records from localities extending from just west of the Precambrian Shield in Manitoba to the vicinity of Banff and Rocky Mountain House, Alberta are available (R. Bell!; F. R. and J. C. Cook!; R. Hartland-Rowe!; M. Ouellet!; Mozley, 1938: 113; and this survey).

Churchill River system. 65 mi S of Fort Churchill, Man. (mile 445, Hudson Bay Railroad) (1929, F. Johansen!). Mouth of Goose Creek, 7 mi S of Churchill. Muskeg, Churchill. Landing Lake, Churchill (all this survey).

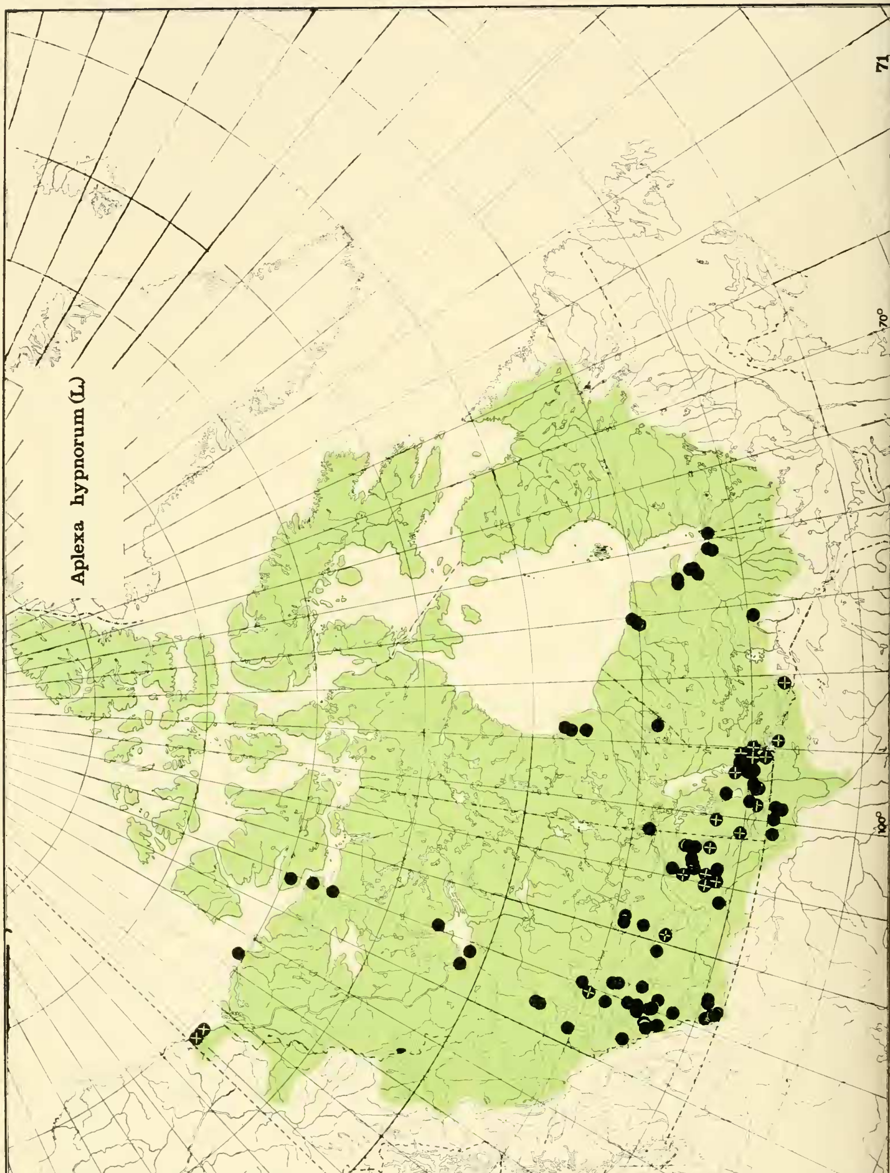
Mackenzie River system. Athabasca River drainage area: Lake near Jasper, Alta. (Mozley, 1938: 113). Pyramid Lake, Jasper National Park, Alta. (1964, Persis and R. W. Coleman!). Creek near Faust, Alta. (Mosley, 1938: 113). Tawatinaw River, 1 mi N of Rochester, Alta. Lesser Slave Lake, Slave Lake, Alta. (both this survey). Peace River drainage area: 3 mi N of Spirit River, Alta. (Mozley, 1938: 113). Swamp near Notikewin River bridge, [near Manning], Alta. (1932, L. S. Russell!). Mackenize River drainage area: Mouth of Hay River, N.W.T. (1919, E. M. Kindle!). 7 mi S of Lady Evelyn Falls, N.W.T.; also Lake Evelyn Falls Junction, N.W.T. 3·6 mi W of Yellowknife, N.W.T. (all 1965, R. Hartland-Rowe!).

Northern Arctic drainage areas. Spring run-off pool near Coppermine River, N.W.T. (67°49′N, 115°06′W) (1957, Fish. Res. Bd.!). Cape Bathurst, N.W.T. (70°35′N, 128°11′W). Pond and river at Bernard Harbour, N.W.T. (68°45′N, 114°45′W). Lake opposite Bernard Habour. Pond, Colville Mountains, Victoria Island, N.W.T. [near 69°35′N, 115°35′W] (all 1915–16, Can. Arctic Exped.!). Small lake, near Sachs Harbour, Banks Island (about 72°N, 125°W) (July 24—August 10, 1958, Fish. Res. Bd.!).

Distribution: New England to District of Columbia, west to the Cascade Mountains, north to James Bay, and northwest to Victoria Island, Banks Island, and Arctic Alaska. *Aplexa hypnorum* appears to be nearly absent from the lime-poor Precambrian Shield but it occurs abundantly within the Shield in the lime-rich Hudson Bay Lowlands (see Map 71). It is also found in Europe and in northern Asia. Geologic range: Early Pleistocene (Nebraskan) to Recent (Hibbard & Taylor, 1960: 121).

Biology and Ecology: The 35 collections of *Aplexa hypnorum* made during this survey are from the following habitats: 10 are from swamps or muskeg, 4 from roadside ditches, 12 from vernal ponds and intermittant streams, 3 from temporarily-flooded marginal areas near permanent streams, 5 from large to medium-sized rivers (only one specimen from each locality), and one (a single specimen) from a large lake. In 8 of the lotic habitats current was slow and in the 3 others it was moderate. Vegetation was thick in most sites but moderate to sparse in some. Bottom sediments were wholly or substantially of mud in all habitats. The densest populations were from muskeg, from spring-flooded areas adjacent to lakes or streams, and from vernal woods pools.

Baker (1928a: 474) writes that "*Aplexa hypnorum* is a species of swales and intermittent streams or stagnant


Aplexa hypnorum (L.)
71
70°
100°
55°
45°

pools in Wisconsin, as far as present data go. It is especially abundant in woodland pools which become dry in summer, in company with *Stagnicola caperata* [=*Lymnaea caperata*], *Physa hildrethiana* [=*P. gyrina*] and *Sphaerium occidentale*. It also occurs...in small clean brooks..." Mozley (1938: 113) writes: "Usually in temporary ponds. Occasionally found in lakes and small slow-flowing streams." See Den Hartog & De Wolf (1962) for details of ecology and life history of *A. hypnorum* in Holland.

The radula, jaw, and genitalia of *Aplexa hypnorum* have been described by Baker (1928a: 471-2). They are similar to *Physa* spp. in most respects. The radula formula is given as 175-1-175 with the central tooth as wide as it is high and with cusps arranged in a 3-1-1-1-3 pattern. Unlike most species of *Physa*, small cusps do not occur between the large cusps on the lateral and marginal teeth. (Baker's fig. 202 is probably of a *Physa* radula; it does not agree with his text). Radulae from specimens collected near Indian Head, Sask. (this survey) agree with Baker's description except that the transition from laterals to marginals, reported to occur at the 10th tooth, is difficult to discern. The animal is dusky-black in colour, has a long, narrow foot and, unlike *Physa*, has no digitations on the mantle.

Remarks: The western arctic populations of *Aplexa hypnorum* seem to be isolated from the principal range of the species and to occupy approximately the same region as the Beringian relict species *Lymnaea kennicotti* and *L. atkaensis*. At first sight these arctic populations appear to have relatively longer apertures and to be morphologically different from southern populations. DeWitt (1954a: 132) has shown that relative obesity in a Michigan population of *Physa gyrina* reared in the laboratory changes with growth. This was not confirmed for the populations studied during this work but it obviously does occur in *A. hypnorum* (see, "Measurements"). Careful examination of Canadian arctic *Aplexa* populations indicates that the specimens differ principally in having fewer whorls (about 5) and in being correspondingly smaller than most more southerly specimens in museum collections. Their L/W and ApL/L ratios are similar to those of partly-grown southern specimens which have about 5 whorls, however. Specimens from the Hudson Bay Lowlands are also smaller than more southern specimens but the contrast is less well-marked. Many arctic specimens do exhibit spiral lines and these are uncommon in most southern populations but this difference is not constant and is not considered significant at the subspecies level.

It appears probable that populations of *Aplexa hypnorum* survived glaciation in the Beringian Refugium but that substantial differences between them and other populations of the species did not evolve. The existence of only 1 boreal-holarctic species of *Aplexa* in 3 continents is further evidence of slow evolution in this genus. Significant physiological differences between arctic and cool-temperate populations of *A. hypnorum* and of other species probably do exist, however, and the need for further research on this problem is evident.

Superfamily Planorbacea

This superfamily is here considered to contain the families Planorbidae and Ancylidae. Although the 2 families differ in important anatomical and shell characters they are more closely related to each other than to the Physidae,

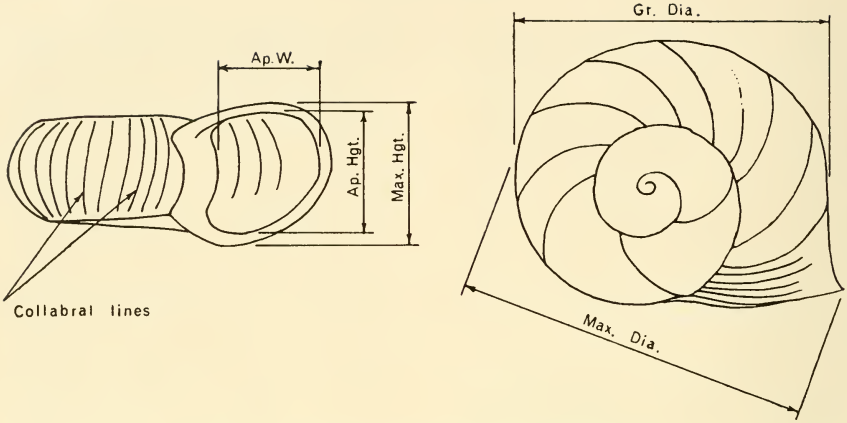


FIG. 9. Definitions of measurements in Planorbidae.

Lymnaeidae,or Acroloxidae. The superfamily is world-wide and occurs only in fresh water.

Family PLANORBIDAE Rafinesque

Planorbidae (correction of "Planorbia") Rafinesque, 1815: *Analyse de la Nature*, p 143 (Binney & Tryon reprint, 1864: 18). Type genus: *Planorbis* Geoffery [=*Planorbis* Müller]. (As subfamily of *Trochinia*).

Shells small to moderately large, thin or slightly thickened, orthostrophic or hyperstrophic, and depressed or planispiral (in most species) or low conispiral (in a few). Aperture oblique, with lip thickened and reflected in some species and with internal lamellae in a few others. The species are monoecious (with facultative cross- and self-fertilization) and phytophagous. Several serve as intermediate hosts for trematodes including human parasites of the genus *Schistosoma*.

"Animal sinistral, having the pulmonary, genital, and excretory orifices on the left side. Tentacles long, slender and cylindrical. Jaw in three [or many] segments. Radula with the numerous teeth arranged in nearly horizontal rows, central small and bicuspid, [also tri- and tetra-cuspid] marginals (*sic*, laterals) tricuspid, laterals [*sic*, marginals] multicuspid" (Walker, 1918: 10).

"The chief feature separating the Planorbidae [except Plesiophysinae] from the other members of the Limnophila is the presence of an accessory breathing organ, the pseudobranch, which takes over the office of a gill when the animal is submerged and can not obtain free air" (Baker, 1945: 50).

Planorbidae are a world-wide family containing about 25 genera and hundreds of nominate species and subspecies. Baker (1945) has published the most important monograph on the family but unfortunately, because of his death, it was not completed at the species level. Baker's results have been extended, re-evaluated, and partly corrected by Hubendick (1955), whose taxonomic system is followed here.

Based on comparative anatomy, Hubendick recognizes 3 subfamilies within Planorbidae, viz., Plesiophysinae, Bulininae, and Planorbinae. Only the Planorbinae are represented in our fauna.

KEY TO SPECIES AND SUBSPECIES OF PLANORBIDAE

1. Shell medium-sized to large (axial height 4 mm or more in post-juveniles) and sinistral or dextral 2
   Shell small (axial height 1 to 4 mm in post-juveniles) and dextral 13
2. Ratio of height to diameter less than 0.4. Diameter 8 to 12 mm. Western United States and Canada . . . . *Planorbula campestris* (Dawson) (p 422, Pl. 13, Figs. 6–8)
   Shell not as above (Genus *Helisoma*) 3
3. Shell dextral . . . . Subgenus *Helisoma* (*s. str.*) 4
   Shell sinistral 5
4. Shell with upper carina heavy and at, or close to, the shoulder. Collabral sculpture coarse . . . . . *Helisoma anceps royalense* (Walker) (p 443, Pl. 25, Figs. 20–22)
   Shell with upper carina variously developed but not close to shoulder. Collabral sculpture moderate to fine . . . . *Helisoma anceps anceps* (Menke) (p 428, Pl. 14, Figs. 1–3)
5. Shell medium-sized (axial height 4 to 7 mm). Aperture bell-shaped . . . . (Subgenus *Planorbella*) 6
   Shell large (axial height 8 mm or more). Aperture flaring, not bell-shaped . . . . . (Subgenus *Pierosoma*) 7
6. Spire flattened or projecting only slightly above body whorl. Spire height less than 5% of body whorl height measured in front of aperture . . . . *Helisoma campanulatum campanulatum* (Say) (p 445, Pl. 13, Figs. 9–11; Pl. 26, Figs. 7–9)
   Spire projecting prominently above body whorl. Spire height more than 10% of body whorl height . . . . *Helisoma campanulatum collinsi* Baker (p 451, Pl. 26, Figs. 10–12)
7. Carinae present at outer edge of upper and lower surfaces of body whorl. Body whorl abaxially flattened, either partly or completely. Western Ontario, Manitoba and Minnesota 8
   Carinae absent or, if present, not at the outer edges of the body whorl. Body whorl abaxially rounded 10
8. Carinae cord-like, strong and acutely angled. Body whorl flat or concave abaxially. Northern Minnesota . . . . *Helisoma corpulentum vermilionense* Baker (p 471, Pl. 27, Figs. 10–12)
   Carinae not cord-like 9
9. Upper surface of shell almost entirely flat Maximum height at aperture 14 mm or more. Ratio of greater height to greater diameter more than 0.75 in many specimens. Headwaters of Rainy River system, Western Ontario . . . . *Helisoma corpulentum whiteavesi* Baker (p 472, Pl. 27, Figs. 13–15)
   Body whorl higher than penultimate whorl, causing spire to be sunken. Maximum height at aperture less than 14 mm. Ratio of greater height to greater diameter less than 0.75. Western Ontario, Minnesota, and Manitoba . . . . *Helisoma corpulentum corpulentum* (Say) (p 465, Pl. 27, Figs. 7–9)
10. Carinae present, at least on early whorls, and near centres of both upper and lower surfaces. Apex depressed, smooth-sided (in many specimens) and bowl-like 11
    Carinae absent, or if present, occurring only on upper surface of whorls and, most commonly, on early whorls only. Apex not bowl-like 12
11. Aperture broadly expanded above and below. Body whorl abruptly higher than penultimate whorl. Alberta and British Columbia . . . . *Helisoma binneyi* (Tryon) (p 463, Pl. 27, Figs. 4–6)
    Aperture expanded above but not below. Body whorl higher than penultimate whorl but not abruptly higher. Western Ontario to Saskatchewan . . . . *Helisoma pilsbryi infracarinatum* (Baker) (p 459, Pl. 14, Figs. 10–12)
12. Axial height (greater height) of adult specimens exceeding 10 mm and, in most specimens, exceeding 12 mm. Eastern Canada and boreal forest region of Western Canada. . . . . . *Helisoma trivolvis trivolvis* (Say) (p 452, Pl. 14, Figs. 4–9; Pl. 27, Figs. 1–3)
    Axial height (greater height) of adult specimens not exceeding 10 mm. Prairie and parkland regions of Western Canada. . . . . . *Helisoma trivolvis subcrenatum* (Carpenter) (p 456, Pl. 26, Figs. 13–15)
13. Shell minute, diameter of adults 2 to 3 mm, peristome complete, and in most specimens with numerous prominant collabral costae which project at the periphery . . . . *Armiger crista* (L.) (p 406, Pl. 25, Figs. 11, 12, 16)
    Shell larger, without costae and peristome incomplete 14
14. Aperture with denticles inside (visible through the aperture or through the shell wall), at least in young juveniles; diameter of adults

exceeding 5 mm, body whorl abaxially rounded, not keeled . . . . Genus *Planorbula* 15
Shell not as above 16

15. Denticles (1 to 4 sets, 5 denticles per set) present in most juvenile specimens. Adults more than 8 mm in diameter. Western United States and Canada south of the boreal forest . . . . . *Planorbula campestris* (Dawson) (p 422, Pl. 13, Figs. 6–8)
Denticles (1 or 2 sets of 6 denticles) present in all stages of growth in most specimens. Adults less than 8 mm in diameter. Eastern Canada and Western Canada inside or close to the boreal forest region . . . . *Planorbula armigera* (Say) (p 419, Pl. 26, Figs. 4–6)

16. Umbilicus prominent, wide, deep, and exhibiting all the whorls; shell diameter in adults 4 to 5 mm; body whorl abaxially rounded. Western United States and Canada south of the boreal forest . . . . *Promenetus umbilicatellus* (Cockerell) (p 415, Pl. 26, Figs. 1–3)
Shell not as above 17

17. Shell flattened and with a prominent, acute peripheral keel; shell not hirsute and sutures not deep; ratio of height to diameter 0.35 or less in adult specimens 18
Shell not as above. Ratio of height to diameter more than 0.35 in adult specimens 20

18. Shell flat apically, convex basally and with an acute keel located high on the body whorl and forming a sharp shoulder. Alberta and British Columbia . . . . *Menetus cooperi* (Baker) (p 417, Pl. 25, Figs. 17–19)
Keel situated medially or medio-basally 19

19. Adult specimens 6 to 8 mm in diameter. Keel very acute and "pinched" or blade-like. Western United States and Canada, principally in the prairie and parkland regions . . . . *Promenetus exacuous megas* (Dall) (p 412, Pl. 25, Figs. 13–16)
Adult specimens 4 to 6 mm in diameter. Keel acute but not "pinched". Throughout most of the Canadian Interior Basin and southward . . . . . *Promenetus exacuous exacuous* (Say) (p 409, Pl. 13, Figs. 3–5)

20. Adult specimens 4 to 7 mm in diameter, variable, with the body whorl not evenly rounded or with a peripheral keel or with a hirsute periostracum or a malleated surface or with any combination of these features . . . . *Gyraulus deflectus* (Say) (p 391, Pl. 25, Figs. 1–4, 7,8)
Adult specimens 3 to 5 mm in diameter, variable, with the body whorl evenly rounded or with upper lateral surface slightly flattened. Without a peripheral keel or a hirsute periostracum or malleated surface 21

21. Shell whitish or yellowish, semi-transparent, entirely or nearly planospiral, appearing almost the same from both sides. Characteristic of aquatic habitats that are subject to periodic drying . . . . *Gyraulus circumstriatus* (Tryon) (p 397, Pl. 25, Figs. 9, 10)
Shell brownish, translucent but not transparent, not planospiral but with apical and umbilical aspects clearly different. Characteristic of permanent and (occasionally) temporary aquatic habitats . . . . *Gyraulus parvus* (Say) (p 400, Pl. 25,. Figs. 5, 6)

Subfamily Planorbinae (*s. str.*)

"Family Planorbidae" of F. C. Baker, 1945.
"Subfamily Planorbinae" of B. Hubendick, 1955.

Planorbinae possess a pseudobranch in contrast to Plesiophysinae in which no pseudobranch is present. They also possess an ordinary penis and not an ultrapenis as in Bulininae.

Hubendick (1955: 523) has grouped the genera of Planorbinae into 4 tribes, the *Planorbis* tribe, the *Segmentina* tribe, the *Biomphalaria* tribe, and the *Helisoma* tribe. Of these only the *Planorbis* and *Helisoma* tribes occur in temperate and subarctic North America. For consistency these tribes are here renamed Planorbini and Helisomatini.

Tribe **Planorbini** (new name)

"Subfamily Planorbinae H. A. Pilsbry" (in part) of Baker, 1945: xiv, etc.
"The *Planorbis* tribe" of Hubendick, 1955: 531.

Planorbinae with short marginal teeth, a separate prostatic duct, a penial stylet in most genera, and no penial flagellae. Of the 5 genera included in this group by

Hubendick i.e., *Planorbis*, *Anisus*, *Gyraulus*, *Armiger* and *Choanomphalus*, only *Gyraulus* and *Armiger* occur in cool-temperate and subarctic North America.

Genus *Gyraulus* Charpentier

Gyraulus "Agassiz" Charpentier, 1837: *Neue Denkschrift, Allgemeine Schweizerische Gesellschaft* (etc.), *1*(2): 21. Type, by subsequent designation (Clessin, 1886: 33). *Planorbis hispidus* Draparnaud [= *Planorbis albus* Müller].

Torquis Dall, 1905: *Land and fresh water mollusks of Alaska and adjoining regions*. Harriman Alaska Exped., (Mollusca) *13*: 83, 86 (as section of subgenus *Gyraulus*). Type species: *Planorbis parvus* Say, by original designation.

Shells small, ultradextral, of comparatively few flattened whorls which are visible both above and below; body whorl in several species characteristically deflected; aperture ovate and prosocline; whorls rounded or carinate and with periostracum which may be or may not be hirsute.

Baker (1945) has discussed in detail the anatomy of several species of *Gyraulus* (*s. str.*) (p. 67-70) and of the subgenus *Torquis* (p. 72-75). Recently, Hubendick (1955: 479) has described additional details of the anatomy of *Gyraulus* species. *Torquis* Dall differs from *Gyraulus* (*s. str.*) in only minor anatomical characters and the name is not used as a separate group designation in the present work. *Gyraulus* is cosmopolitan and according to Baker (1945: 70-71, 75) approximately 100 species are known. Undoubtedly this list will be drastically reduced by future monographic studies. The genus is recorded from deposits as old as the Paleocene (Upper Cretaceous?) of Europe, Asia, North Africa, and North America (Zilch, 1959: 110).

Gyraulus is in need of thorough revision. Inter-population variation is so great that it is often impossible to identify confidently specimens even with the most comprehensive and thoughtful descriptions and keys (Baker, 1928a; 364-384). This is also the opinion of Hanna (1956: 8). No attempt is made in the present work to assess properly the validity of all North American "species" of *Gyraulus*. An effort *is* made however, to evaluate the status of all taxa recorded from the Canadian Interior Basin.

Gyraulus deflectus (Say)

Plate 25, Figs. 1-4, 7, 8; Map 72.

Planorbis deflectus Say, 1824: *Major Long's Second Exped. to source of St. Peter's River*, etc. Vol. 2, Appendix, p 261, pl. 15: 8 (Binney reprint, 1858: 128, pl. 74: 8). Type locality: "waters of the North-West Territory."

Planorbis hirsutus Gould, 1839: *Amer. J. Sci.*, (1) *38*: 196. Type locality: "Dedham [and] Cambridge, [Massachusetts]."

Planorbis obliquus DeKay, 1843: *Zool. New York*, *5*: 62. Type locality: "Mohawk [River] and Newcomb's Pond, Pittstown, [New York]."

Gyraulus hornensis F. C. Baker, 1934: *Can. Field-Naturalist*, *48*: 135, text fig. Type locality: "Birch Lake, Horn River, Mackenzie District."

Diagnosis: Shell small, planorboid, depressed, with slowly enlarging whorls, and with or without a peripheral keel, a hirsute periostracum, or a malleated surface or any combination of these characters.

Description: Shell small to medium-sized (up to about $\frac{1}{3}$ inch in diameter), planorbiform, ultradextral, depressed, pale brown to dark brown, variable in shape and scupture, and with or without hirsute periostracum. Periphery more or less keeled; in many lots the keel is quite pronounced while in other lots the keel is absent. In most specimens the periphery, whether keeled or not, is below the middle of the body whorl. (The only exceptions here recognized as *Gyraulus deflectus* are occasional hirsute specimens corresponding to the *G. hirsutus* of Baker and other authors in which the periphery is centrally located). Periostracum in many speci-

mens covered with hair-like projections arranged in spiral rows approximately parallel to the sutures. In other lots many or all specimens lack a hirsute periostracum, but all are spirally striate to some extent. Sculpture, in addition to spiral striation, consisting of prominent collabral lines of growth and, in some specimens, of narrow, flattened (malleated) spiral bands. Whorls about 4½. Apical whorls sunken below adjacent whorls. Umbilicus wide, shallow, and showing all whorls. Aperture prosocline and subovate except angled adapically and (in keeled specimens) slightly expanded near the periphery. Inner lip with a thin but clearly visible callus.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Fossil Lake, N.W.T. (66°17′N, 128°55′W).					
Diameter, mm	31	4·0 —7·4	6·20	—	—
Height/Diameter *	31	0·26—0·40	0·304	0·005	0·026
No. of whorls	26	3·3 —4·4	3·98	—	—
Periph. keel score **	31	1·0 —1·5	1·29	0·04	0·25
Periost. score **	29	1·0 —1·5	1·19	0·04	0·24
Surf. mall. score **	31	1·0 —1·5	1·18	0·04	0·23
Macklin Lake, Macklin, Sask.					
Diameter, mm	22	3·0 —5·3	4·20	—	—
Height/Diameter	22	0·29—0·38	0·329	0·005	0·025
No. of whorls	27	3·5 —4·5	3·93	—	—
Periph. keel score	27	1·0	—	—	—
Periost. score	27	1·0	—	—	—
Surf. mall. score	27	1·0 —3·0	1·28	0·09	0·49

* Allometric growth occurs in *Gyraulus deflectus*. The smaller specimens tend to have higher height/diameter ratios than the larger specimens.

** See " Remarks " for explanation of the coding system.

Feature	N	Range	Mean	$S.E._M$	S.D.
Small pond near Orient Bay, Lake Nipigon, Ont.					
Diameter, mm	37	2·0 —5·5	3·37	—	—
Height/Diameter	37	0·31—0·46	0·379	0·024	0·147
No. of whorls	37	2·6 —4·5	3·54	—	—
Periph. keel score	39	1·0 —3·0	1·52	0·11	0·66
Periost. score	39	1·5 —4·0	2·92	0·10	0·64
Surf. mall. score	39	1·0	1·00	—	—

Records:

Eastern Hudson Bay and James Bay drainage area. Innuksuak River system: Lake 2 mi N of Inoucdjouac (Port Harrison) Que. Beach drift, south side of unnamed island north of Cairn Island, Richmond Gulf, Que. Outlet of Char Lakes, Richmond Gulf, Que. (56°21′N, 76°30′W) (all this survey). Richmond Gulf, Que. (1960 Fish. Res. Bd.!). Bloody Island Camp, Belcher Islands, N.W.T. (1958, Fish. Res. Bd.!). Trout Pond, Charleton Island, James Bay (1920, F. Johansen!). Eastmain River, Eastmain, Que. Bordeleau River, 20 mi NE of Chibougamau, Que. (both this survey).

Nottaway, Harricanaw, Moose, Albany, Attawapiskat and Winisk River systems. Abundant throughout. Marginal records are: Albany River mouth in tidewater; Attawapiskat River, near Attawapiskat, Ont.; and Winisk River in muskeg pools 6 mi E of Winisk, Ont. (all this survey).

Shell Brook drainage area. Lake at source of Shell Brook, Ont. (55°20′N, 87°17′W) (this survey).

Severn River system. MacDowell Lake, Ont. (52°14′N, 92°47′W). Unnamed lake at 53°37′N, 92°40′W. Swamp near mission, Sandy Lake, Sandy Lake, Ont. (all this survey).

Hayes River system. Stull Lake, at outlet, Ont. (54°29′N, 92°37′W) (this survey).

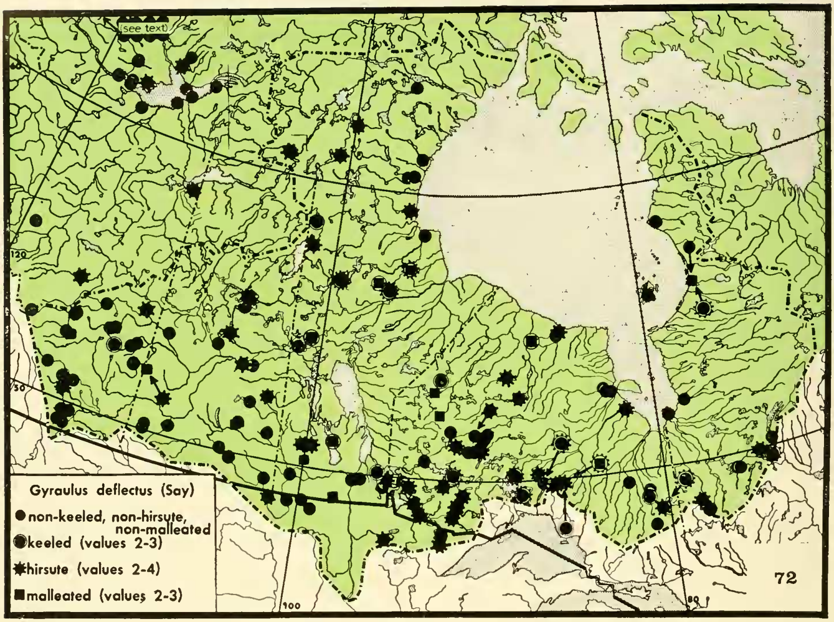
Winnipeg, Red, Saskatchewan, Nelson, and Churchill River systems: Devil's Lake, Lakes Manitoba-Winnipegosis drainage areas. Abundant throughout. Marginal records are: Lower Red Lake, Minn.; Second Vermilion Lake and Minnewanka Lake, Banff, Alta.; Limestone Lake, Man. (56°35′N, 96°00′W); Brochet Lake, Man. (58°35′N, 101°35′W); and Goose Creek, 7 mi S of Churchill, Man. (all this survey).

Western Hudson Bay drainage area. Owl Lake, Man. (56°22′N, 94°35′W). Long Lake, Man. (59°24′N, 95°18′W) (both this survey). Hyde Lake, N.W.T. (60°45′N, 95°22′W) (1959, Fish. Res. Bd.!). McConnell River, 18 mi S of Eskimo Point, N.W.T. (1960, S.D. MacDonald!). Ennadai Lake, SW end, 1 mi N of mouth of Kazan River, N.W.T. (60°45′N, 101°46′W). Angikuni Lake, N.W.T. (62°15′N, 100°00′W) (both this survey).

Nelson River system. Wholdaia Lake, N.W.T. (60°45′N, 104°30′W) (1959, Fish. Res. Bd.!). Baker Lake, 12 mi S of Baker Lake settlement, N.W.T. (1962, R. C. M. P. Cst. E. W. Smith!).

Mainland Central Arctic drainage area. Coppermine River drainage area: Vaillant Lake, N.W.T. (66°12′N, 114°29′W) (1959, Fish. Res. Bd.!). Spring run-off pool, Coppermine River Bluff, N.W.T. (67°49′N, 115°06′W) (1957, Fish. Res. Bd.!). Eskimo Lakes drainage area: Eskimo Lakes [Husky Lakes], N.W.T. (69°32′N, 131°19′W) (1955, Fish. Res. Bd.!).

Mackenzie River system. Peace River drainage area: Pond 6 mi SE of Hythe, Alta. (1963, F. R. Cook!). Athabasca River drainage area: Inlet of Horn Lake, 10 mi SW of Whitecourt, Alta. (this survey). Lake Athabasca (1938, D. S. Rawson!). Liard River drainage area: Dease Lake, B.C. (1962, S. D. MacDonald!). Mackenzie River drainage area: Great Slave Lake and vicinity, numerous localities (1944–46, J. G. Oughton!). Mackenzie River near Fort Providence, N.W.T. (1966, R. W. Coleman!).



Hay River near Hay River, N.W.T. (1917, E. M. Kindle and E. J. Whittaker!). Prelude Lake, N.W.T. (62°34′N, 113°55′W). Yellowknife River 7 mi N of Yellowknife, N.W.T. (both 1966, R. W. Coleman!). Birch Lake, Horn River, N.W.T. (1921, E. J. Whittaker!), Beaver Lake, 30 mi E of Fort Providence. N.W.T. (1921, E. J. Whittaker!). Little Lake [Mills Lake], Mackenzie River (1917, E. M, Kindle!). Keller Lake, N.W.T. (63°59′N. 121°42′W) (1962, Fish. Res. Bd.!). Beaverlodge Lake, N.W.T. (64°39′N, 118°08′W) (1959, Fish. Res. Bd.!). Fossil Lake, N.W.T. (66°17′N, 128°53′W) (1962, Fish. Res. Bd.!). Aklavik, N.W.T. (1933, collector?; 1957, Fish. Res. Bd.!).

Distribution: In North America from the Atlantic Coast (Prince Edward Island to Virginia), west to Alberta and Idaho, south to Ohio and Illinois (Miller, 1966: 231) and north to the vicinity of the Arctic Coast in the Ungava, Coppermine River and Mackenzie River districts (this survey).

Biology and Ecology: *Gyraulus deflectus* was collected at 136 stations during this survey. Of these, 39 stations are large lakes, 25 are small lakes, 11 are permanent ponds, 7 are backwater areas of streams, 9 are rivers over 100 ft. wide 6 are rivers 50 to 100 ft. wide, 16 are rivers 25 to 50 ft. wide, 14 are streams 10 to 25 feet wide, 4 are streams less than 10 feet wide, and 5 are swamps. Unlike *G. circumstriatus* and *G. parvus*, *G. deflectus* was not found in vernal ponds or in roadside ditches which dry out. *G. deflectus* was ordinarily found on submersed vegetation but occasionally on the bottom. Vegetation was moderately abundant to thick in most habitats and the most frequent substrate was mud. In all lotic habitats yielding this species the current in the area occupied was moderate to slow.

Gyraulus deflectus is a characteristic element of most freshwater gastropod faunas associated with eutrophic habitats. In arctic localities with few species its most frequent associates are *Lymnaea arctica* and *Valvata sincera helicoidea*.

The anatomy of *Gyraulus deflectus* has been described by Baker (1945: 67). The soft parts of living specimens recently observed in the laboratory (from Lake Champlain, Vt., shell diameter 6 to 7 mm) are brown, the head is rounded, the tentacles are narrow, tapering and long, the eye spots are prominent, and the shell is carried horizontally or at an angle close to 45°. The foot is short and does not protrude behind the shell during locomotion, which is moderately rapid. The egg capsules are oval, transparent, gelatinous, about 2 mm in diameter, and in the 6 specimens observed contained 2 to 5 eggs.

The radula formulae given by Baker (1945: 69) for *Gyraulus hirsutus* and *G. deflectus obliquus* varies from 19-1-19 to 22-1-22. Specimens from the present research area, which were examined for radula characteristics, gave the following results:

Locality	Cat. No.	Shell Dia., mm	Radula Formula
near Winisk, Ont.	29707	6·2	$\frac{8}{4}-\frac{9}{3}-\frac{1}{2}-\frac{9}{3}-\frac{8}{4}$ (17-1-17)
,, ,, ,,	29150	7·1	$\frac{10}{4\text{-}5}-\frac{9}{3}-\frac{1}{2}-\frac{9}{3}-\frac{9}{4\text{-}5}$ (19-1-18)
near Virginia, Minn.	37148 A	5·5	$\frac{9}{4}-\frac{8}{3}-\frac{1}{2}-\frac{8}{3}-\frac{9}{4}$ (17-1-17)
,, ,, ,,	37148 B	5·0	$\frac{8}{4}-\frac{7}{3}-\frac{1}{2}-\frac{7}{3}-\frac{8}{4}$ (15-1-15)

Remarks: The following arbitrary value scales were used to describe the morphology of the *Gyraulus deflectus* specimens in each lot. (*a*) Peripheral keel: (1) absent, (2) moderately developed, (3) strikingly well-developed. (*b*) Periostracum: (1) not hirsute, (2) slightly hirsute, (3) moderately hirsute, (4) extremely hirsute. (*c*) Surface malleation: (1) not apparent, (2) slightly developed, (3) moderately developed and obvious. Thus (5:2-4-1) means that the lot contains 5 specimens which have (*a*) moderately developed peripheral keels, (*b*) extremely hirsute periostraca, and (*c*) non-malleated surfaces.

In most lots the specimens vary only slightly in these characters and for the purposes of notation the morphology of each lot was expressed by single code numbers (to the nearest 0·5) which are estimated average values for each of the 3 coded characters. The results were too voluminous for complete publication, however, and a summary only is presented (see Map 72). Detailed results are on file at the National Museum of Natural Sciences.

Inspection of the map shows that much inter-population variation occurs but that some trends exist. For example, hirsute morphs are more common in western Ontario than elsewhere and non-keeled, non-hirsute and non-malleated morphs are frequent in Saskatchewan, Alberta, and the Northwest Territories. Far northern populations are predominantly of the latter morphological type. Much randomness is clearly apparent, however, even within the same river system and inter-population variation far exceeds intra-population variation.

A situation analogous to this has been described by Mayr (1956) in terrestrial gastropods of the genus *Cerion* occurring in the Bahama Islands. *Cerion* is an autogamic species living on bushes near the high tide line and new colonies are presumed to be randomly established by transport of 1 or a few individuals to new areas by hurricanes. (Hurricanes also periodically obliterate colonies). Colonies which evolve from these individual introductions are often quite uniform morphologically but may differ remarkably from adjacent colonies.

In *Gyraulus deflectus* adventitious transport by ducks and other aquatic birds is probably of common occurrence (see Rees, 1965). A single individual of this facultative self-fertilizing hermaphroditic species is also potentially capable of founding a new population. The frequency and to a large extent the direction of such transport is probably random and the inter-population morphological variations of the snail are also largely random. This phenomenon and the advantage held by autogamous species in successfully invading new habitats has been discussed previously (Clarke, 1970b).

It is clear from Map 72 that there is complete intergradation between keeled and non-keeled, hirsute and non-hirsute, and malleated and non-malleated populations and that these characters do not vary concordantly. It is also clear that the distribution of similar morphological types is substantially random. It is therefore considered incorrect to recognize any of these morphs as separate species or subspecies (see synonomy).

Dall (1905: 94) and others have suggested that *Gyraulus deflectus* may be synonymous with *G. albus* (Müller) of Europe. Published figures of the latter (e.g., see Adam, 1960: figs. 47, 48) show that keeled and non-keeled morphs exist in a manner similar to that in *G. deflectus*. Miller (1966: 232) has carefully compared *G. deflectus* with *G. albus* in the Museum of Zoology, University of Michigan, and has found consistent differences in surface sculpturing between the 2 species. "*G. albus* has more regularly spaced, raised, spiral and axial ornamentation. The spiral sculpture is better developed and appears as fine lirae resting on the more subdued axial sculpture. In *G. deflectus* the spiral sculpture, when present, is produced by the alignment of impressed pits, which accommodate the hair-like projections in the fresh shell. These pits are lower than the axial growth lines" (Miller, loc. cit.).

I have examined 13 additional lots of *Gyraulus albus* (5 from Europe in the collection of the National Museum of Natural Sciences, 5 from the United States National Museum and 3 from the University of Copenhagen) and all possess the surface sculpturing described above. Some malleated lots of *G. deflectus* show flattened spiral bands, which form low, angular, spiral ridges along their intersecting boundaries, but among the large number of lots available from the research area none have sculpturing similar to that shown

by the lots of *G. albus* examined. The egg masses observed in our laboratory are also smaller than those of *G. albus* as reported by Adam (1960:186). I therefore agree with Miller that *G. deflectus* and *G. albus* are specifically distinct.

Gyraulus circumstriatus (Tryon)
Plate 25, Figs. 9-10; Map 73.

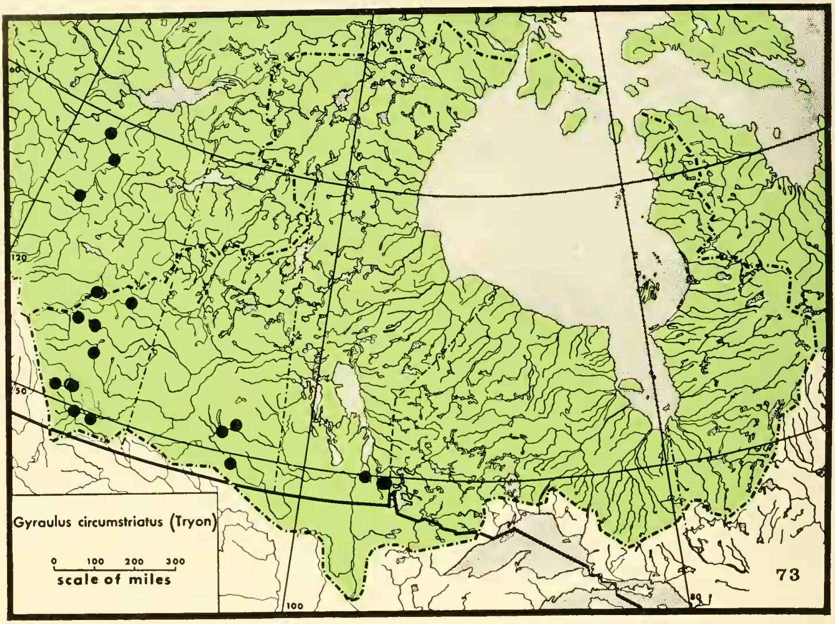
Planorbis (Gyraulus) circumstriatus Tryon, 1866: *Amer. J. Conchol.*, *2*: 113, pl. 10: 6–8. Type locality: " Artificial pond at Weatogue, Conn."
Planorbis parvus walkeri Vanatta, 1902: *Nautilus*, *16*(5): 58. Type locality: " Hartland, Vt."

Diagnosis: Shells small, nearly or completely planospiral, spirally striate in many specimens, semi-transparent, and with rounded whorls which increase slowly in diameter.

Description: Shells small (up to about $\frac{1}{5}$ inch in diameter), low, planorboid (planospiral in many specimens), variable, whitish, transparent to semi-transparent and showing the soft parts inside. Whorls laterally rounded and increasing in size more slowly than in *Gyraulus parvus*. Periostracum smooth and glossy. Fine spiral striae are visible in most specimens, especially on the base. Collabral lines and lines of growth well marked to strong. Whitish collabral streaks present on some specimens. All whorls visible in both apical and umbilical view. Umbilical depression wide, shallow, and in many specimens so similar to the apical depression that except for the configuration of the collabral sculpture and of the aperture the upper and lower views of the shell are essentially mirror images of each other. Aperture prosocline, ovate, and in the same plane as the body whorl or slightly below it. Outer lip thin in most specimens; inner lip without a perceptible callus.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Pond near Falcon Lake, Man.					
Diameter, mm	15	2·4 —4·2	3·30	—	—
Height/Diameter	15	0·29 —0·36	0·312	0·006	0·024
Whorls	15	3·6 —4·2	3·87	—	—
Lac des Lacs, Exshaw, Alta.					
Diameter, mm	13	2·9 —4·5	3·46	—	—
Height/Diameter	13	0·30 —0·34	0·318	0·004	0·015
Whorls	13	3·5 —4·0	3·68	—	—
Tawatinaw River, 1 mi N of Rochester, Alta.					
Diameter, mm	16	2·3 —5·1	3·22	—	—
Height/Diameter	16	0·26 —0·38	0·333	0·008	0·033
Whorls	16	2·9 —4·1	3·41	—	—



Records:

Only specimens examined are included here.

Winnipeg River system. Pond near Falcon Lake, Man. Roadside ditch 10 mi W of Falcon Lake. Pond 6 mi W of Whitemouth, Man. (all this survey).

Red River system. Qu'Appelle Lake, Katepwa Provincial Park, Sask. Creek 4 mi E of Pense, Sask. Tributary of Souris River 2 mi S of Weyburn, Sask. (all this survey).

Inland drainage areas. Small pond among sand hills 12 mi N of North Portal, Sask. (this survey).

Saskatchewan River system. South Saskatchewan River drainage area: 28 mi S of Fort MacLeod, Alta. (1966, R. Hartland-Rowe!). Taber, Alta. (1957, F. R. Cook and J. S. Bleakney!). Lac des Lacs, Exshaw, Alta. Roadside ditch 5 mi N of Carseland, Alta. Slough adjoining Eagle Lake, 3 mi SE of Strathmore, Alta. Pond 12 mi S of Namaka, Alta. (all this survey). North Saskatchewan River drainage area: Pond 1 mi E of Lindbrook, Alta. Pond 2 mi E of Poe, Alta. Outlet of Cache Lake, 2 mi W of Spedden, Alta. (all this survey).

Mackenzie River system. Athabasca River drainage area: Marsh 4½ mi W of Rochester, Alta. Tawatinaw River, 1 mi N of Rochester (both this survey). Peace River drainage area: Swamp near Notikewin River bridge, [Manning], Alta. (1932, L. S. Russell!). Melito Creek, Alta. (59°38′N, 117°10′W) (1965, R. Hartland-Rowe!). Hay River drainage area: 6 mi S of Steen River, Alta. (59°38′N, 117°10′W) (1965, R. Hartland-Rowe!).

Distribution: Connecticut north to Quebec, west to Alberta and south in the Rocky Mountains to New Mexico. Its precise geographical limits have not been determined.

Biology and Ecology: Living specimens of *Gyraulus circumstriatus* were collected at only 14 stations during this survey. Of these, 7 are ponds of doubtful permanence (during June, 1965, a wet month, all had water in them), 2 are roadside ditches which almost certainly dry out in late summer, 1 is a swamp,

and 4 are small creeks also of doubtful permanence. At nearly all localities vegetation was moderate to thick and the substrate was of mud. These observations agree with those of Taylor (1960: 57) who states that "*Gyraulus circumstriatus* is characteristic of small, seasonal water bodies, such as wood pools, marshes, ponds on flood plains or prairie ponds. In northern Nebraska it was found in seepages beside streams, and in temporary Sand Hills pools."

Species most frequently associated with *Gyraulus circumstriatus* are *Lymnaea elodes*, *L. caperata*, *G. parvus*, *Physa gyrina* (*s. str.*) *Physa jennessi skinneri*, and *Sphaerium lacustre*.

Baker (1945: 73-74, pl. 17: 1-5) has discussed and figured the anatomy of this species. It was found to be similar in all characters examined to other species of *Gyraulus*. Baker gives 14-1-14 as the radula formula for specimens from Wainwright, Alta. Two specimens collected during the present survey had radula formulae as follows:

Locality	Cat. No.	Shell Dia., mm	Radula Formula
Near Falcon Lake, Man.	27950 C	4·0	$\frac{7}{4}-\frac{9}{3}-\frac{1}{2}-\frac{9}{3}-\frac{7}{4}$ (16-1-16)
Near North Portal, Sask.	29103 B	3·1	$\frac{7}{4}-\frac{7}{3}-\frac{1}{2}-\frac{7}{3}-\frac{6}{4}$ (14-1-13)

Burch (1960a) gives the haploid chromosome number as 36 and the diploid number as approximately 72 for specimens of *Gyraulus circumstriatus* from Michigan. That is twice the usual number of chromosomes found in planorbids and indicates that *G. circumstriatus* is probably a polyploid (i.e., tetraploid). See Burch & Huber (1966) for a summary of polyploidy in molluscs.

Gyraulus circumstriatus shows much less morphological variability and much less tolerance for diverse ecological conditions than either *G. deflectus* or *G. parvus*. It appears probable that polyploidy in this species may have selective advantage by acting as a buffer against genetically controlled variability, which otherwise might produce individuals which are less well adapted for successful existence in the specialized environment occupied by *G. circumtriatus*.

Remarks on Unidentified Material: Specimens resembling *Gyraulus circumstriatus* have also been collected from Recluse Lake, Manitoba (56°55′N, 95°45′W) and from 2 localities in Goose Creek near Churchill, Man. They are pale and translucent and exhibit the shallow umbilical opening typical of *G. circumstriatus* but the whorls enlarge a little too rapidly for that species and the body whorl is deflected downward rather too much for *G. circumstriatus*. In the latter characteristics they resemble *G. parvus*. Because of these uncertainties they have been left as unidentified. It is of interest, however, that both localities are in a limestone region isolated from the main range of *G. circumstriatus* by the Precambrian Shield. The specimens may represent atypical *G. circumstriatus*, atypical *G. parvus*, or even an undescribed species.

Remarks on *Gyraulus circumstriatus walkeri*: This taxon was described by Vanatta (1902: 58, as *Gyraulus parvus walkeri*) as follows: "This variety is similar to *P.* [*lanorbis*] *parvus* but distinguished by having the lip internally thickened." Vanatta cited the "variety" from 7 localities in Michigan. Later Pilsbry (*in* Winslow, 1926: 15) transferred *walkeri* to varietal status under *G. circumstriatus*.

In 1929 Walker (p 104) described a "subspecies" of the western *Gyraulus vermicularis* (Gould) (named *G. v. hendersoni*) collected from a ditch at Phoenix, Oregon; from Loon Lake, 38 mi N of Spokane, Washington; and from a lagoon 14 mi SW of Spokane. He wrote: "In general appearance similar to the typical form, but smaller and with a varix or callus deposit inside the lip...This form bears the same relation to typical *vermicularis* that var. *walkeri* does to *G. parvus* [sic.]."

Among material from the research area lots containing some specimens of *Gyraulus* with thickened apertures were seen from the following localities: Gull Lake, Gull Lake, Alta. (*Gyraulus deflectus* and *G. parvus*); Hanson's Creek, 6 mi E of Rennie, Man. (*Gyraulus deflectus*, hirsute morph); Tenaille Lake, 15 mi N of Maple Creek, Sask. (*G. deflectus*); "Little Lake" [Mills Lake], Mackenzie River, N.W.T. (61°25′N, 118°10′W) (*G. deflectus*). Four species of *Gyraulus* therefore are known in which the thickened lip condition occurs, viz., *G. deflectus*, *G. circumstriatus*, *G. parvus*, and *G. vermicularis*. Perhaps significantly, none of these thickened morphs are recorded from the lime-poor Precambrian Shield.

Ecological information is lacking for most of the published localities for this morph but the sporadic nature of its occurrence, the multiplicity of "species" exhibiting this character, and information regarding similar variation in other species and its probable causes indicate that lip thickening of the type described in *Gyraulus* is ecophenotypic and indicative of depauperization, not genetic or of taxonomic significance. It is well known, for example, that species with a wide tolerance for diverse water hardnesses characteristically exhibit thicker shells in hard water than in soft (see, e.g., Goodrich, 1939). It is reasonable to assume that gyraulids living in lime-rich habitats which periodically undergo great changes in hardness through evaporation may be expected to reflect these changes by periodic thickening. Parallel cases have been described in other molluscan families in which morphological responses have been much more extreme, e.g. in Lymnaeidae (Baker, 1911: 2) and in Ancylidae (Basch, 1963b). *G. circumstriatus walkeri* is therefore almost certainly not a valid subspecies and does not appear to merit taxonomic recognition.

Gyraulus parvus (Say)
Plate 25, Figs. 5, 6; Map 74.

Planorbis parvus Say, 1817: *Nicholson's Encyclopedia*. 1st Amer. ed., pl. 1, fig. 5 (Binney reprint 1858: 45). Type locality: "very numerous in the Delaware [River, near Philadelphia]."
Gyraulus latistomus Baker, 1932: *Nautilus*, *46*(1): 9. Type locality: "McAree Lake, Rainy River District, western Ontario, Canada."

Diagnosis: Shell small, planorboid, depressed but not planospiral, whorls increasing with moderate rapidity, with rounded periphery, and without prominent striation or hirsute periostracum.

Description: Shell small (up to about 1/5 inch in diameter), planorbiform, ultradextral, depressed, pale brown to dark brown, variable in shape but without prominent striation, a peripheral keel, or hirsute periostracum. Periphery

rounded and located close to the centre of the body whorl. Periostracum of fresh, clean specimens smooth (except for lines of growth) and glossy. Spire flat with the first 2 whorls depressed. Umbilicus wide, shallow, " reamed-out ", and exhibiting all the whorls. Aperture prosocline, ovate, and in the same plane as the body whorl or somewhat deflected below it. Outer lip thin (in most specimens); inner lip with a thin callus.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Klotz Lake, 30 mi E of Longlac, Ont.					
Diameter, mm	11	1·5 —3·0	2·23	—	—
Height/Diameter *	11	0·35—0·53	0·431	0·016	0·054
Whorls	11	2·7 —4·0	3·31	—	—
Rolling River, near Campbell Lake, 8 mi NE of Erickson, Man.					
Diameter, mm	22	3·1 —4·1	3·57	—	—
Height/Diameter	22	0·31—0·46	0·346	0·007	0·034
Whorls	22	3·4 —3·8	3·55	—	—
Lake, Broughton Island, Nastapoka Islands, N.W.T.					
Diameter, mm	30	2·1 —4·5	3·52	—	—
Height/Diameter	30	0·29—0·46	0·371	0·008	0·044
Whorls	30	2·7 —3·9	3·50	—	—

* As in *Gyraulus deflectus* allometric growth occurs. Small specimens tend to give higher Height/Diameter values than larger specimens.

Records:

Ungava Bay drainage area. Koksoak River drainage area: Lac Aigneau, Que. (1955, D. R. Oliver!). Fort Chimo, Que. (1896, W. Spreadborough!).

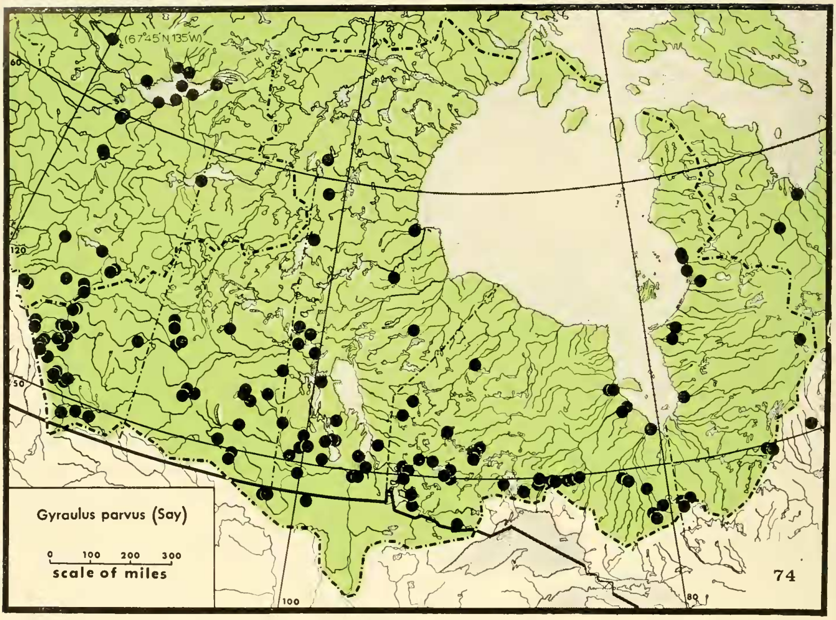
Eastern Hudson Bay and eastern James Bay drainage areas. Small lake, north-central Broughton Island; pond, south end of Ross Island: and small lake and outlet, southern Mowat Island, all Nastapoka Islands, N.W.T. Pond near Clearwater River, ¾ mi E of Richmond Gulf. Burton Lake, N side, 33 mi SSW of Poste de la Baleine (Great Whale River), Que. Middle Fork, Roggan River, 73 mi SSW of Poste de la Baleine (Great Whale River) Que. (all this survey). Headwaters of Fort George River, Nitchequon, Que. (1962, R. Goodland and W. K. W. Baldwin!). Woods pools, Eastmain, Que. (this survey).

Chibougamau River system. Caché Lake near Chibougamau, Que. (this survey).

Moose and Albany River systems. Common throughout. Marginal records are from a pond near Moose Factory, Ont. (1920, F. Johansen!) and 4 localities in the vicinity of Fort Albany, Ont. (all this survey).

Attawapiskat River system. Attawapiskat River at side channel, 6 mi W of Attawapiskat, Ont. Monument Channel at portage, 20 mi W of Attawapiskat (both this survey).

Severn River system. MacDowell Lake, Ont.



(52°14′N, 92°47′W). Deer Lake, Deer Lake, Ont. South end, Severn Lake, Ont. (54°00′N, 90°40′W) (all this survey).

Hayes River system. Knee Lake at northern narrows, Man. (55°04′N, 94°45′W) (this survey).

Winnipeg, Brokenhead, Red, and Saskatchewan River systems; Devil's Lake, and Lake Manitoba and Lake Winnipegosis drainage areas. Abundant throughout the whole region (85 NMC records).

Nelson River system. Lake St. Martin, 3 mi SE of Gypsumville, Man. (1964, M. Ouellet!). Lake Winnipeg, 20 mi S of Gimli, Man. River near Petersfield, Man. O'Hanly River, 18 mi N of Pine Falls, Man. Lake 27 mi E of Simonhouse, Man. Stout Lake at outlet, Ont. (52°08′N, 94°44′W) (all this survey).

Churchill River system. Pond 30 mi S of Meadow Lake, Sask. (1962, F. R. Cook and C. B. Powell!). Montreal Lake, S end, 16 mi N of Waskesiu, Sask. Goose Creek (2 localities) 7 mi S of Churchill, Man. (all this survey).

Western Hudson Bay drainage area. Kasmere Lake, Man. (59°35′N, 101°10′W). Ennadai Lake, SW end, N.W.T. (60°45′N, 101°46′W) (both this survey).

Mackenzie River system. 10 mi S of Little Smoky, Alta. High Level, Alta. ½ mi S of Steen River, Alta. (all 1965, R. Hartland-Rowe!). Annette Lake, Mildred Lake, and Patricia Lake, near Jasper, Alta. (1954, F. H. Schultz and J. C. Ward!). Horseshoe Lake, 10 mi SE of Jasper (this survey). 9 mi S of Mayerthorpe, Alta. (1965, R. Hartland-Rowe!) Lesser Slave Lake, Slave Lake, Alta. Marsh 4½ mi W of Rochester, Alta. Tawatinaw River, 1 mi N of Rochester, Alta. Baptiste Lake, 12 mi W of Athabasca, Alta. (all this survey), Camsell Portage, Lake Athabasca (from whitefish stomachs) (1945, D. S. Rawson!). Near Hay River, 11 mi and ¼ mi S of 60th parallel (both 1965, R. Hartland-Rowe!). Great Slave Lake and vicinity, several localities (1944–46, J. G. Oughton!). Long Lake, near Yellowknife, N.W.T. (1966, R. W. Coleman!). Beaver Lake, 30 mi E of Fort Providence, N.W.T. (1921, E. J. Whittaker!).

Distribution: " North America, from Alaska and northern Canada to Cuba and from the Atlantic to the Pacific

coast. Perhaps also in northern Eurasia" (Taylor, 1960: 58). In Canada its northern limit corresponds fairly well with the tree line, i. e. the northern limit of the boreal forest.

Biology and Ecology: *Gyraulus parvus* was collected at 104 localities during this survey. Of these 31 sites are in large lakes, 17 in small lakes, 5 in permanent ponds, 3 in vernal ponds, 4 in backwater areas of streams, 1 in a roadside ditch, 3 in swamps, 11 in rivers over 100 feet wide, 4 in rivers 50 to 100 feet wide, 14 in rivers 25 to 50 feet wide, 6 in streams 10 to 25 feet wide and 5 in streams less than 10 feet wide. Specimens were almost always found on aquatic vegetation. Bottom types were diverse but mud was most frequent, occurring at 60% of the stations. In all lotic habitats the current was slow to moderate.

Species often found associated with *Gyraulus parvus* are *Lymnaea stagnalis*, *L. elodes*, *Physa* spp., *G. deflectus*, *Promenetus exacuous*, *Amnicola limosa*, etc.

The anatomy of *Gyraulus parvus* has been described by Baker (1928a: 376 and 1945: 72). The soft parts of the living animal are similar in general appearance to those of *G. deflectus*. Baker (1945: 74) gives the radula formula as 14-1-14. Specimens from the research area had radulae as follows:

Locality	Cat. No.	Shell Dia., mm	Radula Formula
Broughton I., Hudson Bay	19523 A	4·3	$\frac{11}{4-5}-\frac{6}{3}-\frac{1}{2}-\frac{6}{3}-\frac{11}{4-5}$ (17-1-17)
,, ,,	19523 B	4·0	$\frac{10}{4-5}-\frac{6}{3}-\frac{1}{2}-\frac{6}{3}-\frac{9}{4-5}$ (16-1-15)
near Hanna, Alta.	32455 A	3·5	$\frac{7}{4-5}-\frac{7}{3}-\frac{1}{2}-\frac{7}{3}-\frac{6}{4-5}$ (14-1-13)
,, ,,	32455 B	4·7	$\frac{7}{4-5}-\frac{6}{3}-\frac{1}{2}\ \ \frac{6}{3}-\frac{7}{4-5}$ (13-1-13)

Remarks: Examination of a paratype of *Gyraulus latistomus* Baker in the National Museum of Natural Sciences (NMC 3207) and comparison of Baker's original description has convinced me that this name is a synonym of *G. parvus*. The paratype appears to have been deformed through injury during growth and the body whorl behind the aperture is bent downward.

Mozley (1938: 109) has recorded *Planorbis* (*Gyraulus*) *arcticus* "Beck" Müller from numerous localities in Canada, from the Mackenzie River District in the Northwest Territories and the Sioux Lookout District in Ontario. These records are based on specimens previously identified by Baker and published by Whittaker (1924) and by Baker & Cahn (1931). Baker (1934: 135) later revised his concept of *G. arcticus* after an examination of a Greenland specimen identified as *Planorbis arcticus* by Mörch and concluded that specimens which he had previously reported as *G. arcticus* belonged to other species. The records republished by Mozley are therefore omitted here.

Eastern populations here identified as *Gyraulus parvus* appear to be slightly more flattened along the upper peripheral side of the body whorl, than

PLATE 25. Planorbidae (I)

FIGS. 1–3. *Gyraulus deflectus* (carinate morph), Wapikapa Lake, northern Ontario (NMC 2231 5·5 mm). . . . . p 391

FIGS. 4, 7, 8. *Gyraulus deflectus* (hirsute morph), pond near Orient Bay, Lake Nipigon, Ontario (NMC 19346, 4·8 mm). . . . . p 391

FIGS. 5, 6. *Gyraulus parvus*, N shore Clear Lake, Manitoba (NMC 21935, 4·0 mm). . . . . p 400

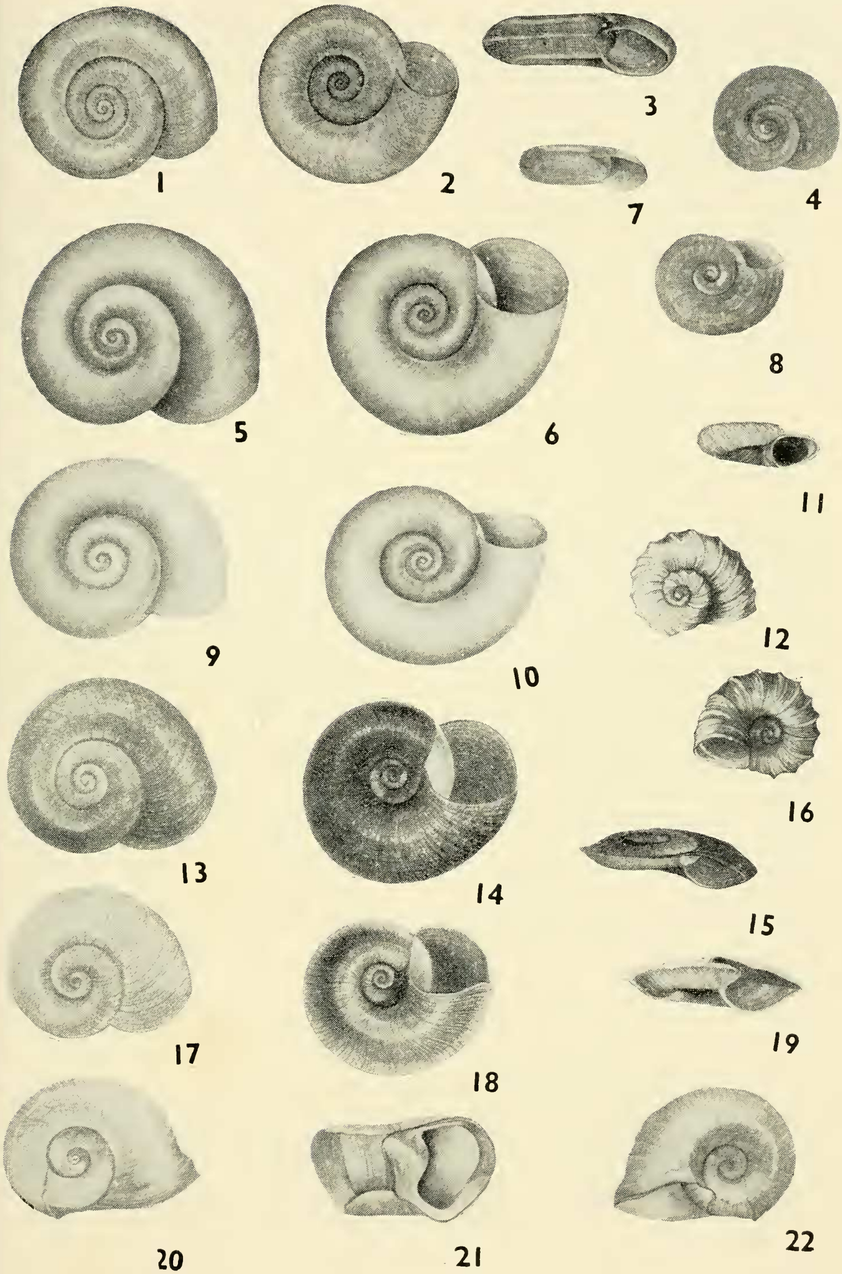
FIGS. 9, 10. *Gyraulus circumstriatus*, Lac des Lacs, Exshaw, Alberta (NMC 29096, 3·4 mm). . . . . p 397

FIGS. 11, 12, 16. *Armiger crista*, Marean Lake, Saskatchewan (NMC 28674, 1·8 mm) . . . . p 4C6

FIGS. 13–15. *Promenetus exacuous megas*, Tisdale, Saskatchewan (NMC 383351, 5·8 mm). . . . . p 412

FIGS. 17–19. *Menetus cooperi*, Whitney Lake, near Lindbergh, Alberta (NMC 32335, 5·6 mm). . . . . p 417

FIGS. 20–22. *Helisoma anceps royalense*, Abram Lake, Sioux Lookout Ontario (NMC 25663, 13·4 mm). . . . . p 443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western specimens and it is possible that further work will reveal the presence of 2 taxa and may even result in the eventual recognition of *G. arcticus* or of *G. similaris* Baker. Much time was spent during this work in an effort to find consistent differences which would validate these taxa but without avail. Unfortunately even positive differentiation of *G. parvus* from some specimens of *G. circumstriatus* and *G. deflectus* is not always easy. Revision of the difficult genus *Gyraulus* is especially desirable.

Genus *Armiger* Hartmann

Armiger Hartmann [1840] 1843: *Erd-und Süss-wasser-Gasteropoden*. p 172. Type species, by monotypy, *Nautilus crista* L.

Shells minute, in general like *Gyraulus*, but with a complete peristome and, in most specimens, with numerous, prominent, peripheral axial costae. Anatomically *Armiger* is also similar to *Gyraulus* but possesses a small penial papilla on one side of the sperm outlet. Although controversy exists regarding the taxonomic importance of the anatomical differences (Odhner, 1929: 20-21, 30; Baker, 1945: 78, Hubendick 1955: 466), on shell characters alone this group appears to merit separate generic status.

Armiger is holarctic in distribution and contains about 4 species. Stratigraphically the genus has been recorded from deposits of Miocene to Recent age (Zilch, 1959:112). It appears frequently in Pleistocene (Wisconsin) sediments in North America (La Rocque, 1964: (14) 26, etc.).

Armiger crista (Linnaeus)

Plate 25, Figs. 11, 12, 16; Map 75.

Nautilus crista Linnaeus, 1758: *Systema Natura*, 10th ed., p 709. Type locality: " in Germaniae paludibus " [in German marshes]. See Dall, 1905: 96 and Baker 1928a: 385 for a list of synonyms from the European literature.

Diagnosis: Shell minute, planorboid, and ordinarily with numerous costae which project prominently at the periphery.

Description: Shell very small (about $\frac{1}{8}$ inch in diameter), thin, depressed, planorbiform, ultradextral, pale brown, and with numerous narrow costae and very fine, spiral lines. Costae parallel to lines of growth, about 12 to 18 in number on each whorl, inclined forward, and projecting as triangular periostracal lamellae at the periphery of the body whorl. (In fossil specimens the periostracum is absent and the peripheral projections are nodular). Whorls $2\frac{1}{2}$ in adults, rapidly increasing in size, flattened above, rounded below, and angularly rounded at the periphery. Umbilicus wide, deep, and showing all previous whorls. Aperture prosocline, subelliptical, and wider than high. Lip thin and complete (holostomous).

Measurements:

Feature	N	Range	Mean
Creek 12 mi W of Bottineau, N.D. (recently dead).			
Diameter, mm	2	2·7 —3·0	2·85
Height/Diameter	2	0·30—0·33	0·315
Whorls	2	2·5 —2·7	2·60
Body Whorl Costae	2	12—20	16·0

Feature	N	Range	Mean
Barrier Lake, near Archerwill, Sask. (subfossil).			
Diameter, mm	6	2·0 —2·7	2·20
Height/Diameter	6	0·30—0·37	0 330
Whorls	6	2·2 —2·7	2·38
Body Whorl Costae	6	13—22	15·9
Pond 1 mi E of Lindbrook, Alta. (living).			
Diameter, mm	6	1·5 —2·5	2·17
Height/Diameter	6	0·30—0·35	0 320
Whorls	6	2·0 —2·5	2·32
Body Whorl Costae	6	0 —15	3·67

Records:

Moose River system. Pond near Moose Factory, Ont. (living) (1920, F. Johansen!).

Red River system. Creek 12 mi W of Bottineau, N.D. (empty but fresh specimens) (this survey). Lady Lake, Lady Lake, Sask. (living) (1965, Donald J. Buckle!). Whitesand River, 9 mi ESE of Sheho, Sask. (subfossil) (this survey).

Lake Manitoba and Lake Winnipegosis drainage area. Marean Lake, near Archerwill, Sask. (subfossil) and Barrier Lake, also near Archerwill, Sask. (subfossil) (both 1964, D. L. Delorme!). Lake Manitoba, east side, 15 mi W of Benhorn, Man., also 1 mi N of Narrows (both subfossil). Lake Winnipegosis, Denbeigh Point, Man. (subfossil) (both 1964, M. Ouellet!).

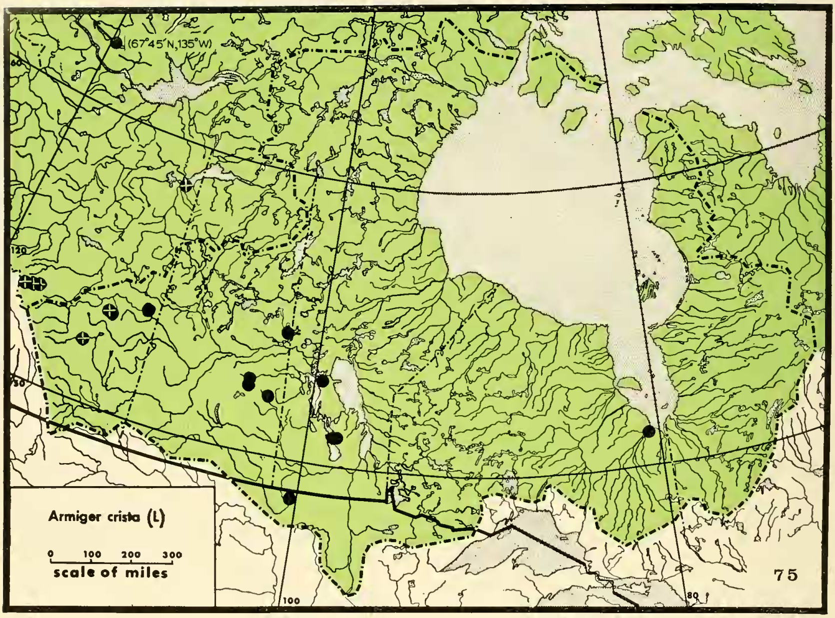
Saskatchewan River system. [Near] Red Deer, Alta. (Dall, 1905: 97). Pond 1 mi E of Lindbrook, Alta. (living). Pond 2 mi E of Poe, Alta. (living) (both this survey). [Near] Tofield, Alta. (Mozley, 1938: 109). Whitney Lake, 6 mi SE of Lindbergh, Alta. (empty fresh specimens) (this survey).

Nelson River system. "Excavation above Big Island, Dillman Marl, near Flin Flon [Manistikwan Lake], Man." (subfossil) (1939, T. L. Tanton!).

Athabasca River system. Virl Lake,, Trefoil Lake, and Lake No. 6, all near Jasper Alta. Athabasca Delta, Alta. (all Mozley, 1938: 109).

Distribution: Holarctic, recorded from Europe, northern Asia, North Africa, and from scattered localities in the northern United States (Maine to Minnesota), Canada (Ontario to Alberta and northwestern Northwest Territories), and Alaska (Fort Yukon, Dall, 1917: 12).

Biology and Ecology: During this survey *Armiger crista* was found living at only 2 localities, a pond 2 mi E of Poe, Alta. and another pond 1 mi E of Lindbrook, Alta. The ponds are very similar: each is eutrophic, about 2 acres in area, surrounded by *Typha* and grass, with thick submersed vegetation (mostly *Potamogeton*) and with a mud bottom. *A. crista* was taken from the submersed vegetation in 1½ to 2½ feet of water in the 1st pond and 8 inches of water in the second. A slow-moving creek 12 mi W of Bottineau, N.D., which produced apprently fresh, uneroded, empty shells, is 30 feet wide, choked with *Typha* and grass, and has a mud bottom overlain with dead *Typha* stalks. Each of these localities supported rich populations of *Gyraulus*, *Promenetus*, *Lymnaea*, etc. See Ökland (1964: 161) for details of the ecology of *A. crista* in Norway.



The anatomy and reproduction of *Armiger crista* has been described by Moquin-Tandon (1855: 438) and discussed in detail by Baker (1945: 76). The radula formulae of European specimens are reported to vary from 11-1-11 to 16-1-16 and the egg capsules are reported to be about 1·5 mm in diameter and to contain 3 to 6 eggs.

Remarks: There is a substantial variation in the shell morphology of this species. Costae may be strongly developed, weakly developed, absent, or prominent on some parts of a specimen and absent on others. The most strongly costate specimens seen were sub-adult. Two of the specimens from near Lindbrook, Alberta, had the body whorl partially detached; in 1 this whorl was free for $\frac{1}{4}$ of its length. Such diversity was also noticed in British specimens by Jeffreys (1862: 83) and in Norwegian specimens by Ökland (1964 : 161).

In the Canadian Interior Basin and probably in North America as a whole, *Armiger crista* appears to be rare and local in distribution. Although the minute size of this species would contribute to its being easily overlooked, during the present survey nets with 1 mm mesh were used which would have retained *A. crista* if it had been encountered. However, among several hundreds of stations sampled which appeared to be ecologically suitable, this species was found at only 3.

The relative abundance of *Armiger crista* in North America appears to have declined substantially since the Pleistocene. La Rocque (1964: (14) 26) lists 18 eastern North American localities from which this species has been

recorded, but 15 of these are from Pleistocene sediments (mostly of Wisconsin age) and only 3 represent living specimens. This trend is apparent from museum collections as well.

It is probably significant that no Pleistocene or Recent records exist for the whole Precambrian Shield. With 1 exception, the only eastern North American records are from south of the Hudson Bay drainage area and south of the edge of the Shield, i.e., Ottawa and Hamilton, Ontario; Barren Brook, Maine; and Monroe County, New York. The single exception is the record from near Moose Factory, Ontario, an isolated region containing calcareous deposits, and separated from the other known Ontario *Armiger* localities by nearly 400 miles of lime-poor Precambrian Shield country. This kind of distribution is seen in some other species also, e.g., *Sphaerium occidentale*, *Ferrissia rivularis* and *Lymnaea modicella*. Possible causes for this interesting pattern are discussed in the Introduction.

Tribe **Helisomatini** (new name)

"Subfamily Helisomatinae Baker" + "Subfamily Planorbulinae Pilsbry", of Baker, 1945: xv etc.
"The *Helisoma* tribe" of Hubendick, 1955: 534.

Planorbinae with long lateral radular teeth, specialized male copulatory organs, and evolved prostate glands. Genera included here are *Helisoma*, *Promenetus*, *Menetus* and *Planorbula*, all occurring in the present research area, and *Planorbarius*, *Parapholyx* and *Carinifex*, all extralimital.

Genus *Promenetus* F.C. Baker

Promenetus F. C. Baker, 1935: *Nautilus*, *49*: 48. Type species, by original designation, *Planorbis exacuous* Say.

Phreatomenetus D. W. Taylor, 1960: [United States] *Geol. Surv. Prof. Paper*, 337: 60 (as subgenus of *Promenetus*). Type species: *Promenetus umbilicatellus* (Cockerell), by original designation.

Shells small, ultradextral, planorboid, depressed, whorls few and rapidly increasing in diameter, carinate or rounded, umbilical area broad or moderately broad and showing all whorls, spire flattened, and aperture wider than high. The anatomy is much like that of *Planorbula*.

Five Recent species and 1 subspecies of the North American genus are recognized (Baker, 1945: 182). Geologic range: Pliocene to Recent (Taylor, 1960: 23).

Only 2 species of *Promenetus* have been studied anatomically, viz., *P. exacuous* (Say) and *P. umbilicatellus* (Cockerell) and their anatomies are very similar. They are, therefore, the only species which can be assigned to *Promenetus* with certainty. The 2 species do differ conchologically in that *P. exacuous* has flattened and carinate whorls whereas *P. umbilicatellus* has rounded whorls. *Promenetus* is such a small genus, however, and shells of Planorbidae show so much variability between species that to recognize *Phreatomenetus* as a subgenus of *Promenetus* is not considered prudent at this time, especially in view of the relatively conservative policy adopted throughout this work.

Promenetus exacuous exacuous (Say)
Plate 13, Figs. 3-5; Map 76.

Planorbis exacuous Say, 1821: *J. Acad. natr. Sci. Philad.*, *2*: 168 (Binney reprint, 1858: 64) Type locality: "Inhabits Lake Champlain."

Diagnosis: Shell planorbiform, small, flattened, biconvex, and acutely angled at the periphery.

Description: Shell small (up to about $\frac{1}{4}$ inch in diameter), flattened, planorbiform, ultradextral, pale brown to dark

brown, and with the outer edge of the body whorl acutely angled. In many specimens this angle is sharply keeled; in others the keel is present but rounded. Keel close to or below the centre of the body whorl. Whorls about 4 in adults and rapidly increasing in size. Spire low-convex or flattened. Sculpture of fine lines of growth (which may be slightly elevated) and fine spiral lines. Umbilicus narrow, deep, and exhibiting all the whorls. Aperture prosocline, obtusely triangular or ovate, and expanded near the periphery. Outer lip thin to slightly thickened. Inner lip with a thin callus.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Pond, 1 mi E of Lindbrook, Alta.					
Diameter, mm	30	2·0 —6·0	4·43	—	—
Height/Diameter	30	0·25—0·35	0·292	0·004	0·021
Whorls	30	2·7 —3·9	3·22	—	—
Lake Winnipeg, 20 mi S of Gimli, Man.					
Diameter, mm	17	2·1 —5·0	3·41	—	—
Height/Diameter	17	0·24—0·33	0·289	0·005	0·022
Whorls	17	2·4 —3·5	3·02	—	—
Klotz Lake, 30 mi E of Longlac, Ont.					
Diameter, mm	20	2·4 —6·9	4·55	—	—
Height/Diameter	20	0·24—0·33	0·270	0·004	0·019
Whorls	18	2·7 —3·9	3·35	—	—

Records:

Only records based on specimens personally examined are listed below. For additional locality records see Mozley (1938: 108) and La Rocque (1964: 30).

Moose River system. Lillabelle Lake, 5 mi N of Cochrane, Ont. Abitibi River, 17 mi N of Cochrane, Ont. (both this survey). Pond at Moose Factory, Ont. (1920, F. Johansen!).

Albany River system. Klotz Lake, 30 mi E of Longlac, Ont. Small lake, 3 mi N of Geraldton, Ont. Pools on bank of Albany River, Fort Albany, Ont. Yellow Creek and nearby pond, near Fort Albany, (all this survey).

Attawapiskat River system. Kawinogans River, Ont. (1904, W. McInnes!). Monument Channel at points 20 mi W and 12 mi W of Attawapiskat, Ont. Muskeg near north bank of Attawapiskat River, 1 mi E of Attawapiskat, Ont. (both this survey).

Winisk River system. West end of Shibogama Lake (53°31′N, 88°35′W), Ont. (this survey).

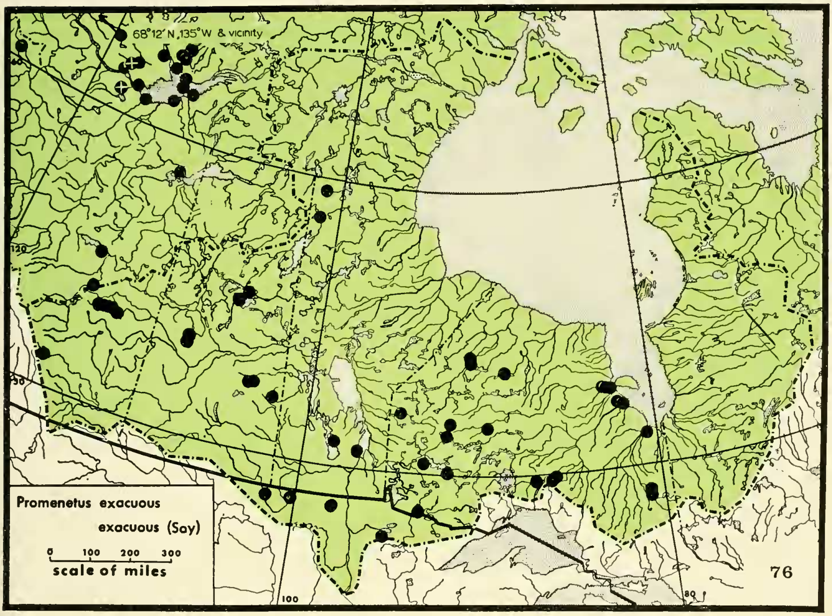
Severn River system. Severn Lake, south end (54°00′N, 90°40′W) and north end (54°05′N, 90°42′W), Ont. (both this survey).

Winnipeg River system. Rainy Lake, 2 mi E of Fort Frances, Ont. (this survey). Cat Lake Ont. (1929, A. R. Cahn!). Bamaji Lake in cove on island, Ont. (51°10′N, 91°25′W), Sturgeon River [=Marchington River] 1 mi W of Superior Junction, Ont. Pelican Lake, Sioux Lookout, Ont. Wabaskang Lake, 40 mi N of Vermilion Bay, Ont. (all this survey).

Red River system. Lower Red Lake, 1 mi S of outlet, 40 mi NNW of Bemidji, Minn. Marsh 9 mi W of Langdon, N.D. Souris (" Mouse ") River 15 mi WNW of Mohall, N.D. (all this survey). Lady Lake, Lady Lake, Sask. (1961, D. J. Buckle!).

Devil's Lake drainage area. (Inland drainage area). Creek 12 mi W of Bottineau, N.D. (this survey).

Lake Manitoba—Lake Winnipegosis drainage area. Lake Manitoba, east side, 1 mi N of Narrows, Man. Denbeigh Point, NE part of



Lake Winnipegosis, Man. (both 1964, M. Ouellet!). Barrier lake and Marean Lake, Sask. (subfossil) (both 1964, D. L. Delorme!).

Saskatchewan River system. South Saskatchewan River drainage area: Second Vermilion Lake, Banff, Alta. (this survey). North Saskatchewan River drainage area: Seba Beach, Wabamun Lake, Alta. (1926, L. S. Russell!). Horseshoe Bend, North Saskatchewan River, Edmonton, Alta. (1925, L. S. Russell!). Slough, Edmonton, Alta. (1962, J. E. Moore!). Pond 1 mi E of Lindbrook Alta (this survey). Pond at Glaslyn and 14 mi N of Glaslyn, Sask. (both 1962, F. R. Cook and C. B. Powell!).

Nelson River system. Lake Winnipeg, 20 mi S of Gimli, Man. Stout Lake, at outlet, Ont. (52°08′N, 94°44′W) (both this survey).

Churchill River system. Midway Lake, 12 mi N of La Ronge, Sask. Twin Lake, 35 mi N of of La Ronge, Sask. Brochet Lake, east end (58°35′N 101°35′W), Man. (all this survey).

Tha-Anne River system. Kasmere lake (59°35′N, 101°10′W), Man. (this survey).

Mackenzie River system. Wabash Creek, 3 mi W of Westlock, Alta. Lesser Slave lake, Slave Lake, Alta. (both this survey). Second Lake, Horn River, Mackenzie River District, N.W.T. (Whittaker, 1924: 11). Birch Lake, Horn River, N.W.T. (1921, E. J. Whittaker!). Great Slave Lake, several localities (1944–46, J. G. Oughton!). Mills Lake, Mackenzie River, N.W.T. (1917, E. W. Kindle!). North Toobally Lake, Y.T. (60°20′N, 126°15′W) (1961, P. M. Youngman!). Lake Kakisa near mouth of Kakisa River, N.W.T. (Whittaker, 1924: 11). Fossil Lake, N.W.T. (66°17′N, 128°55′W) (1962, E. M. Innes!). Lakes 30 mi S of Aklavik, N.W.T. (1940, K. H. Lang!). Aklavik, (1933, collector?).

Distribution: " United States east of the Rocky Mountains, north to Alaska and the Mackenzie River, south to New Mexico " (Baker 1928a: 363). Present records indicate that it is absent from the Quebec part of the research area but occurs widely west of James Bay and Hudson Bay, principally south of the tree-line.

Biology and Ecology: This species was found in several kinds of habitats during the survey. Fifteen lots came from large lakes, 4 from small lakes, 2 from a permanent pond, 4 from large rivers, 1 from a creek 30 feet wide, 1 from a creek backwater, and 3 from swamps. Vegetation was moderately thick to thick at all localities, bottom types were diverse but most were of mud, and in all lotic environments the current was slow in the area occupied by this species. Mozley (1938: 108) gives " temporary ponds, small lakes, marshes, and the bottom of large lakes, e.g., Lake Winnipegosis " as the habitat for *Promenetus exacuous exacuous*.

The anatomy of this species has been described by Baker (1928a: 362; 1945: 178). The radula formulae reported are 16-1-16 and 17-1-17. One specimen from a pond near Lindbrook, Alta. (NMC 29309B) 3·9 mm in diameter, had the formula $\frac{10}{4}-\frac{8}{3}-\frac{1}{2}-\frac{8}{3}-\frac{10}{4}$ (18-1-18).

Promenetus exacuous megas (Dall)
Plate 25, Figs. 13-16; Map 77.

Planorbis (*Menetus*) *exacuous* variety *megas* Dall, 1905: *Land and fresh water mollusks of Alaska and adjoining regions.* Harriman Alaska Exped., *13*: 91. Type locality: " Birtle, Manitoba. "

Diagnosis: Shell planorbiform, small-medium (diameter about $\frac{1}{3}$ inch), convex apically and flat basally, or biconvex and with peripheral keel sharply acute or blade-like.

Description: This subspecies differs from *Promenetus exacuous exacuous* principally by the much larger size and heavier shell of adult specimens. Much variation in shape can be seen but in general subadult specimens of *P. e. megas* can be distinguished by having the peripheral keel more acute and " pinched " than in *P. e. exacuous.* This is variable however, and it is a character which occurs over a greater geographical area than gigantism, the most obvious character of *P. e. megas.* In many specimens of *P. e. megas* the periostracum extends beyond the apex of the keel in a blade-like lamina. This is visible only in fresh or alcoholic specimens but it has not been seen in the *P. e. exacuous* collected during this survey. The spiral striae also appear to be more strongly marked in *P. e. megas* and in many specimens the upper surface of the shell is slightly dome-shaped and the lower surface is almost flat. Except for size, however, present observations have revealed no characters which individually will always distinguish *P. e. megas* from *P. e. exacuous* except perhaps the laminate periostracal extension seen on the few lots preserved in alcohol.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Pond, 4·3 mi N of Twin Butte, Alta.					
Diameter, mm	30	3·5 —7·7	5·66	—	—
Height/Diameter	30	0·24 —0·31	0·270	0·003	0·017
Whorls	28	3·1 —3·9	3·61	—	—

Feature	N	Range	Mean	S.E.$_M$	S.D.
Pond, 3·5 mi N of Salvador, Sask.					
Diameter, mm	4	5·6 —8·3	7·08	—	—
Height/Diameter	4	0·24 —0·26	0·251	—	—
Whorls	3	3·6 —4·1	3·87	—	—
Pond, 1 mi E of Indian Head, Sask.					
Diameter, mm	13	4·9 —8·8	6·92	—	—
Height/Diameter	13	0·20 —0·25	0·229	0·004	0·016
Whorls	12	3·5 —4·0	3·76	—	—
Roadside ditch, 8 mi NW of Rolla, N.D.					
Diameter, mm	17	3·3 —5·8	4·95	—	—
Height/Diameter	17	0·24 —0·27	0·255	0·002	0·010
Whorls	17	3·1 —3·8	3·59	—	—

Records:

Because of possible confusion of the two sub-species only specimens seen are included. For additional locality citations see La Rocque (1964: 30).

Red River system. Assiniboine River drainage area: Whitesand River, 7 mi E (living) and 9 mi ESE (subfossil) of Sheho, Sask. Moose Jaw Creek, 5 mi WSW of Milestone, Sask. Creek 1 mi E of Indian Head, Sask. Creek 4 mi E of Pence, Sask. (all this survey). Small lake in sand hills, W of Pine Creek and NE of Carberry, Man. (1906, J. Macoun). Birtle, Man. (type locality). Pond 1 mi N of Minnedosa, Man. (this survey). Red River drainage area: Stream 6 mi SW of Oak Bluff, Man. (this survey).

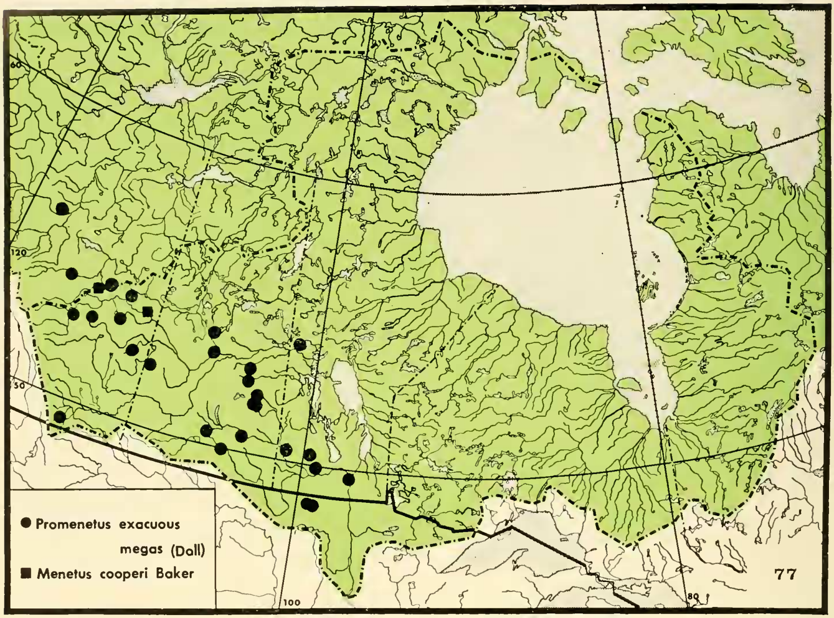
Devil's Lake drainage area. (Inland drainage area). Rock Lake, 18 mi E of Rolla N. D. Roadside ditch, 8 mi NW of Rolla, N. D. (both this survey).

Lake Winnipegosis drainage area. Pond, Lintlaw, Sask. (1962, F. R. Cook and C. B. Powell!). Kipabiskau Lake, Sask. (1964, D. Delorme !).

Saskatchewan River system. South Saskatchewan River drainage area: Pond 4 mi N of Twin Butte, Alta. (1963, J. C. Cook !). North Saskatchewan River drainage area: Pond 2 mi E of Poe, Alta. Pond 1 mi E of Lindbrook, Alta. Ribstone Creek, 5 mi W of Metiskow, Alta. Cache Lake outlet 2 mi W of Spedden, Alta. (all this survey). Pond 3½ mi N of Salvador, Sask. (1962, F. R. Cook and C. B. Powell!). Shell River, 6 mi W of Prince Albert, Sask. Halkett Lake, 20 mi S of Waskesiu Lake, Sask. (both this survey). Tisdale, Sask. (1962, F. R. Cook and C. B. Powell !). Root Lake, 19 mi N of The Pas, Man. (this survey).

Mackenzie River system. Peace River drainage area: Leith River [=Little Burnt River], 2 mi NNW of Whitelaw, Alta. Athabasca River drainage area: Inlet of Horn Lake, 10 mi SW of Whitecourt, Alta. Tawatinaw River, 1 mi N of Rochester, Alta. (all this survey).

Distribution: According to Baker (1928a: 364) this is a " northern form found principally in Wisconsin, Minnesota, and Canada." In Canada it occurs sporadically throughout the southern part of the huge Red River-Saskatchewan River-Nelson River system and in the extreme southern part of the Mackenzie River system from east-



central Manitoba to west-central Alberta. Baker (1945: 181) also reported it from south-central British Columbia. In the United States it extends at least as far west as North Dakota (see above).

Biology and Ecology: The 18 lots of living *Promenetus exacuous megas* collected during this survey came from diverse habitats, as follows: (*a*) 2 lots were from medium-sized lakes, (*b*) 1 from a small lake, (*c*) 3 from permanent ponds, (*d*) 1 from a roadside ditch, (*e*) 1 from a ponded portion of a small stream, (*f*) 1 from a swampy creek, (*g*) 2 from swamps, (*h*) 5 from small to medium-sized slow flowing streams 15 to 100 feet wide and (*i*) 2 from more rapidly flowing streams of intermediate width. In habitats (*b*) and (*i*) the bottom was sandy and vegetation was moderate or sparse but in all other habitats the bottom was of mud and vegetation was thick. *P. e. megas* was most abundant in the roadside ditch near Rolla, N.D., in the swampy creek near Indian Head, Sask., and in the small weed-filled Moose Jaw Creek near Milestone, Sask. Baker (1928a: 364) cites this as " largely a lake form " but such is not the case in Canada.

Associated gastropods often include *Gyraulus* spp., *Planorbula campestris*, and *Lymnaea elodes*.

The anatomy of *Promenetus exacuous megas* is reported to be like that of *P. e. exacuous* (Baker, 1928a: 364 and also see Baker, 1945:178). One specimen from a pond near Poe, Alberta (NMC 29794), 5·6 mm in diameter, had the radula formula $\frac{10}{4\text{–}5} - \frac{7}{3\text{–}4} - \frac{1}{2} - \frac{7}{3\text{–}4} - \frac{10}{4\text{–}5}$ (17-1-17).

Remarks: The geographical ranges of both *Promenetus exacuous megas*, (the large-shelled subspecies of *P. e. exacuous*) and *Planorbula campestris* (the large-shelled *Planorbula*) occupy roughly the same region. Both taxa also occur in approximately the same habitats. This suggests that the same unknown selective forces which permit or encourage comparatively large size may be operative in both cases.

Promenetus umbilicatellus (Cockerell)
Plate 26, Figs. 1-3; Map 78.

Planorbis umbilicatus Taylor, 1885: *J. Conchol.*, *4*: 351, text figs. Type locality: " Brandon, Birtle, etc., Manitoba."

Planorbis umbilicatellus Cockerell, 1887: *Conchol. Exch.*, *2*: 68. New name for *Planorbis umbilicatus* Taylor, 1885, non Müller, 1774.

Diagnosis: Small, planorbiform, and with a prominent, deep, wide umbilicus, spiral striae, and a subtriangular aperture.

Description: Shell small (about 1/5 inch in diameter), depressed, planorbiform, dextral, pale yellowish to brownish, and with a glossy surface sculptured with fine collabral lines and fine revolving striae. Whorls about $4\frac{1}{4}$ in adults, regularly increasing in diameter except slightly expanded near the aperture. Spire flattened or with the first 2 whorls slightly depressed below successive whorls. Sutures deeply impressed. Base of body whorl flatly rounded. Umbilicus prominent, large, deep, and showing all whorls. Aperture rounded, sub-triangular. Outer lip narrow and parietal wall with thin callus.

Measurements:

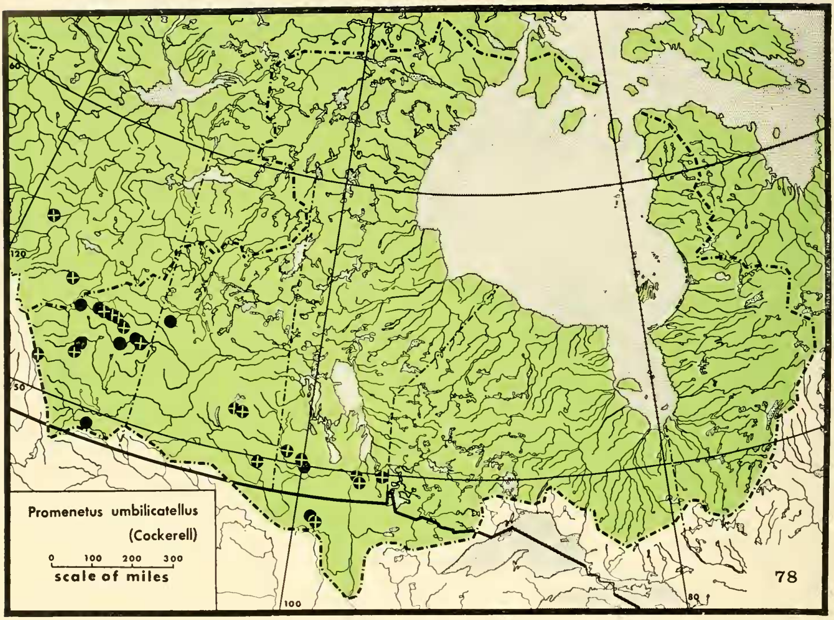
Feature	N	Range	Mean	S.E.$_M$	S.D.
Near Brandon, Man. (syntypes).					
Diameter, mm	7	3·2 —4·8	4·13	—	—
Height/Diameter	7	0·38—0·42	0·399	0·006	0·016
Whorls	7	3·3 —4·0	3·70	—	—
4 mi S of Galahad, Alta.					
Diameter, mm	10	4·2 —5·1	4·49	—	—
Height Diameter	10	0·38—0·42	0·394	0·005	0·015
Whorls	10	3·5 —4·0	3·79	—	—

Records:

Although many of the vernal ponds, roadside ditches etc., occupied by *Promenetus umbilicatellus* have no outlets and are therefore not part cf riversy stems, for consistency of presentation the river system arrangement of listing records is retained.

Winnipeg River system. Brereton [Lake], Man. (Mozley, 1938: 109).

Red River system: Red River drainage area: St, Vital and Grande Pointe, Man. (both Mozley, 1938: 109). Assiniboine River drainage area: Kelliher, Sask. and small lakes and ponds in Moose Mountain Forest Preserve, Sask. (both Mozley, 1938: 109). Pond 3 mi E of Parkbeg, Sask. (this survey). Birtle, Man. (Taylor, 1885: 351). Rapid City, Man. (Dall, 1905: 96). Brandon, Man. (1885, R. M. Christy !, " cotypes " of *Planorbis umbilicatus* Taylor).



Devil's Lake drainage area. (Inland drainage). Near Devil's Lake (Winslow 1921: 12). Marsh north of Lac aux Morts (1919, M. Winslow !).

Quill Lakes drainage area. (Inland drainage). Touchwood, Sask. (Mozley, 1938: 109). 5 mi W, 1 mi S and 3 mi S of Wrentham, Alta. (3 localities). (1966, R. Hartland-Rowe !).

Saskatchewan River system. South Saskatchewan drainage area: Laggan [=Lake Louise], Alta. and Red Deer, Alta. (both Dall, 1905: 96). Waskasoo Creek, 3 mi S of Penhold, Alta. (this survey). Olds, Alta. (Dall, 1905: 96). North Saskatchewan drainage area: Seba [Beach], Alta. (date ?, A. Mozley !). Irma, Alta. (1953, A. Mozley !). Edmonton, Alta. (1924, Owen Bryant !). Ponds near Cooking Lake, Alta. Tofield, Shonts, Viking and Wainwright, Alta. (all Mozley, 1938: 109). Pond 4 mi S of Galahad. Alta. Roadside pond 30 mi S of Meadow Lake, Sask. (both 1962, F. R. Cook & C. B. Powell !).

Pakowki Lake drainage area. (Inland drainage). 10·3 mi N of Stirling, Alta. (1966, R. Hartland-Rowe !).

Mackenzie River system. Athabasca River drainage area: McLeod [River], Alta. (Dall, 1905: 96). Peace River drainage area: 3 mi N of Spirit River, Alta. (Mozley, 1938: 109).

Distribution: Recorded from New Mexico to Manitoba and Alberta (Vanatta 1896: 117; Mozley, 1938: 109).

Biology and Ecology: According to Mozley (1938: 109) " *P. umbilicatellus* occurs only in temporary ponds. " Two collections of this species were made during the present survey from Waskasoo Creek, 3 mi S of Penhold, Alta. and from a pond 3 mi E of Parkbeg, Sask. The creek was slow-moving, muddy, and contained much tall grass in (and adjacent to) the water. It had flooded its banks when visited on June 18, 1965 and although its normal stream bed appeared to be about 20 feet wide it probably dries up during summers of low precipitation. The pond was about ½ acre in area when

visted on June 10, 1965, and was densely vegetated, principally by arrowweed and grass. It appears to be vernal. One other locality for which some ecological data are available is a roadside pond 30 mi S of Meadow Lake, Sask. When visited on July 4, 1962, it was a small, boggy pond with sphagnum, tall grass, and submersed vegetation. The limited information available from 3 additional localities therefore corroborates Mozley's observations and extends the known range of favourable localities to include sluggish, intermittant streams.

Baker (1935: 46) has shown that *Promenetus umbilicatellus*, long regarded as a *Gyraulus*, is anatomically similar to *P. exacuous* and concluded that it should be considered congeneric with it. For details of its anatomy see Baker (1945: 178-181). The radula formula is stated to be 17-1-17 or 18-1-18.

Genus *Menetus* H. & A. Adams

Menetus H. & A. Adams, 1855: *The Genera of Recent Mollusca* (etc.). *2*: 262. Type species, by subsequent designation (Dall, 1870: 351), *Planorbis opercularis* Gould.

Shells small, ultradextral, planorboid, depressed, of few rapidly enlarging whorls, body whorl much larger than preceding whorls, shoulder with sharp or rounded carination, spire whorls immersed, aperture wide and expanded. Anatomically the penis is sac-like with a short, narrow, internal duct and an ephiphallus-like enlargement of the vas deferens as it enters the vergic sac. The prostate and ovotestis are like those of *Planorbula* and the radula and jaw are like those of *Planorbula* and *Promenetus*. The penis and penial duct are quite unlike those of *Planorbula* and *Promenetus*, however.

Hubendick (1955: 491) has asserted that Baker's (1945: 183-7) description of the male reproductive organ of *Menetus* is wrong. He based this decision on an examination of specimens from Chippewa County, Michigan, identified as *Menetus opercularis* (Gould). *M. opercularis* is a far-western species which does not occur in Michigan, however, and the specimens examined were probably *Promenetus exacuous* (Say).

Three Recent species and 2 Recent subspecies of *Menetus* are recognized, all from west of the Rocky Mountains and central Alberta. Geologically the genus is known from the Pliocene to the Recent in North America.

Menetus cooperi Baker

Plate 25, Figs. 17-19; Map 77.

Planorbis planulatus W. Cooper, 1859: (*in*) G. Suckley & J. G. Cooper, *nat. Hist. Wash. Territ.* (etc.). New York, pt. 3, (6) p 378. Type locality: " lakes of Whidby's Island at the entrance of Puget Sound. "

Menetus cooperi F. C. Baker, 1945: *The Molluscan Family Planorbidae*. p 186 (new name for *Planorbis planulatus* Cooper, 1859, non Deshayes, 1825). For a more complete synonymy see Dall, 1905: 92.

Diagnosis: Shell small, planorboid, flat apically, convex basally and with an acute peripheral keel located at the shoulder of the body whorl.

Description (of Alberta specimens): Shell resembling *Promenetus exacuous* except that the peripheral keel is located high on the body whorl and forms a sharp shoulder; it is not located medially or basally. Shell small (about ¼ inch in diameter), flattened above and rounded below, dextral, and pale yellowish-brown to dusky brown. Keel bounded by a wide, shallow groove above and below. Whorls nearly 4, rapidly expanding. Spire slightly depressed below body whorl which is weakly convex above and strongly convex below. Sculpture of fine spiral lines

and slightly heavier lines of growth. Umbilicus broad, shallow and exhibiting all the whorls. Aperture prosocline, subtriangular, and expanded laterally. Outer lip thin. Parietal wall with a thin callus above and below.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Wabash Creek, 3 mi W of Westlock, Alta.					
Diameter, mm	2	3·0, 4·1	3·55	—	—
Height/Diameter	2	0·32, 0·33	0·325	—	—
Whorls	2	2·8, 3·2	3·00	—	—
Whitney Lake, 6 mi E of Lindbergh, Alta.					
Diameter, mm	30	4·0 —6·8	5·63	—	—
Height/Diameter	30	0·24—0·32	0·269	0·003	0·018
Whorls	30	3·2 —3·7	3·51	—	—

Records:

Saskatchewan River system. Whitney Lake, 6 mi E of Lindbergh, Alta. (this survey).

Mackenzie River system. Wabash Creek, 3 mi W of Westlock, Alta. (this survey).

Distribution: " Northern California to Vancouver Island " (Baker 1945: 186). " Puget Sound to Alaska " (La Rocque, 1953: 292). Now also recorded from Central and Eastern Alberta.

Biology and Ecology: Wabash Creek near Westlock is about 25 feet wide and 1½ feet deep (on July 15, 1965) with dark-stained water, sparse vegetation, slow current, and sand bottom. Whitney Lake near Lindbergh has an area of about one square mile and at the site visited on July 15, 1965 (beach at southwest shore) the bottom was of sand and vegetation was absent. All specimens found (2 at Wabash Creek and about 70 at Whitney Lake) were empty shells from drift but they were uneroded and appear to be from currently living populations. Other species occurring at Wabash Creek were *Helisoma trivolvis subcrenatum*, *Promenetus exacuous exacuous*, and *Sphaerium lacustre*. At Whitney Lake *Gyraulus deflectus*, *Physa gyrina*, *Pisidium lilljeborgi* and 13 other less-numerous species were also found.

The anatomy of *Menetus cooperi* has been described by Baker (1945: 183). The radula formula is given as 20-1-20.

Genus *Planorbula* Haldeman

Discus Haldeman, 1840: *A Monograph of the Limniades* (etc.). Pt. 1 p 4 of cover. Type species, by monotypy, *Planorbis armigerus* Say.

Planorbula Haldeman, 1840: op. cit. Supp. to Pt. 1, p 2. New name for *Discus* Haldeman, 1840, *non* Fitzinger, 1833 (Molluscs).

" *Segmentina* Fleming " of authors but not of Fleming 1817: *Edinburgh Encyclopedia*, Conchology, ed. 7, *12*. Type species, by monotypy, *Nautilus lacustris* Lightfoot (= *Planorbis nitibus* Müller). *Segmentina* is the type genus of a distinct subfamily of Planorbidae, the Segmentininae (Baker, 1945; see also Hubendick, 1955).

Shells medium-sized to small, dextral, planorboid, with rounded or subcarinate whorls, and with at least 1 set of 5 to 6 lamellae within the aperture at some stage of growth. Baker (1945: 177) states that " The chief characteristics of *Planorbula* are the ovate or rounded penial gland without an external duct but with a canal-like duct within the preputium, and the prostate with small, branched diverticula on one side of the main diverticulum. Its nearest relative is *Promenetus*, with which it agrees in general in the form of prostate and penial gland. "

About 4 nominate Recent species of *Planorbula* are known, all from temperate or subarctic North America. The genus is recorded from Pleistocene deposits as old as Nebraskan or Aftonian (Taylor, 1960: 33).

Planorbula armigera (Say)

Plate 26, Figs. 4-6; Map 79.

Planorbis armigerus Say, 1821 [1818]: *J. Acad. natr. Sci. Philad.*, *2*: 164 (Binney reprint, 1858: 63). Type locality: " Inhabits Upper Mis. [souri River]."

?*Planorbis lautus* H. Adams, 1861: *Proc. zool. Soc. London*, p. 145. Type locality: " New Orleans".

?*Planorbis jenksii* Carpenter, 1871: Central Falls Visitor, March 2, 1887; *Conchol. Exch.*, *2*: 2. Type locality: " near Hammond's Pond, Pawtucket. R.I. "

?*Segmentina crassilabris* Walker, 1907: *Nautilus*, *20*: 122, pl. 7: 4-6. Type locality: " near Hamtramck, Mich. "

?*Planorbula armigera* var. *palustris* Baker, 1931: *Nat. Mus. Can., Bull.* 67: 58. Type locality: " pond at Camp Colfax, near La Porte, Ind. "

Diagnosis: Shell planorbiform, small, whorls rounded and subcarinate, spire somewhat concave, body whorl bent downward near aperture, and with 6 unequal tooth-like processes within and behind the aperture.

Description: Shell small (about $\frac{1}{4}$ inch in diameter), planorbiform, dextral, pale brown to blackish, and with fine lines of growth and partly obscure, microscopic spiral striae. Whorls about 5 in adults, rounded, but with an obscure carina above and below. Spire markedly concave. Umbilicus wide, deep, funnel-shaped and exhibiting all the whorls. Last part of body whorl expanded and abruptly deflected downward. Lip thin to slightly thickened. Aperture ovate, prosocline and at an angle of about 45° with respect to the umbilical axis. Within the aperture of most specimens, about $\frac{1}{4}$ whorl back, are 6 unequal tooth-like processes. One on the parietal wall is broad and much larger than the others (see Pl. 26, Figs. 4-6). These processes are visible under magnification in apertural view or, if the shell is clean, by light transmitted through the shell wall. Rarely, 2 sets of denticles are present, 1 behind the other (Miller, 1968: 262; also NMC specimens).

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Fossil Lake, N.W.T. (66 17'N, 128 55'W).					
Diameter, mm	20	6·0 —8·5	7·46	—	—
Height/Diameter*	20	0·34—0·40	0·386	0·006	0·028
Whorls	20	4·2 —5·0	4·41	—	—

* As in some other planorbids allometric growth occurs; small specimens exhibit higher H/D ratios than large specimens.

Feature	N	Range	Mean	S.E.$_M$	S.D.
Playgreen Lake, Man. (54°00′N, 98°10′W).					
Diameter, mm	30	5·8 —7·8	7·14	—	—
Height/Diameter	30	0·36—0·45	0·405	0·003	0·018
Whorls	30	4·1 —4·9	4·21	—	—
Small stream 3½ mi E of Finland, Ont.					
Diameter, mm	21	2·6 —7·9	5·01	—	—
Height/Diameter	21	0·38—0·66	0·513	0·020	0·092
Whorls	20	2·8 —4·8	3·58	—	—
Attawapiskat River, 1 mi E of Attawapiskat, Ont.					
Diameter, mm	23	4·4 —7·8	5·93	—	—
Height/Diameter	23	0·36—0·48	0·397	0·006	0·030
Whorls	23	3·5 —4·9	4·15	—	—

Records:

Only specimens seen are listed here. For some additional records from the area as here defined see Dall, 1905: 98; Baker & Cahn, 1931: 58 and 1939b: 98; Mozley, 1938: 110; and La Rocque 1964: 30.

Albany River system. North end of Long Lake, Longlac, Ont. Kenogamisis Lake, 7 mi SE of Geraldton, Ont. Hutchinson Lake, 5 mi N of Geraldton, Ont. (all this survey). Hamilton Lake, Ont. (51°51′N, 90°28′W) (1929 A. R. Cahn !). Yellow Creek and pond south of Albany River, near Fort Albany, Ont. Creek on small island NNE of E end of Anderson Island, Fort Albany. Marsh, south shore, mouth of Albany River (all this survey).

Attawapiskat River system. Fitchie Lake, Ont. (50°37′N, 90°32′W) (1929, A. R. Cahn !). Kawinogans River, Ont. (51°39′N, 89°55′W) (1904, W. McInnes !). Muskeg 1 mi E of Attawapiskat, Ont. (this survey).

Winisk River system. W end of Shibogama Lake, Ont. (53°31′N, 88°35′W) (this survey).

Severn River system. Severn Lake, N end (54°05′N, 90°42′W) and S end (54°00′N, 90°40′W) of lake, Ont. Deer Lake near Deer Lake trading post, Ont. (52°09′N, 94°00′W), North Spirit Lake, at outlet, Ont. (52°31′N, 93°02′W). Swamp near mission, Sandy Lake, Sandy Lake, Ont. (all this survey).

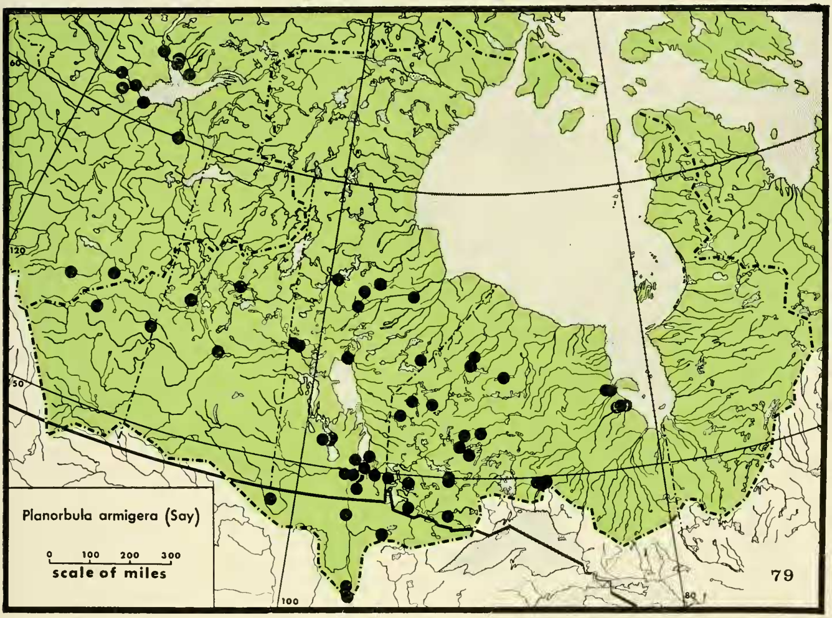
Hayes River system. Muskeg adjoining Red Sucker Lake, Man. (54°10′N, 93°57′W) (this survey).

Winnipeg River system. Bamaji Lake, Ont. (51°09′N, 91°25′W) (1929, A. R. Cahn !). Pelican Lake, Sioux Lookout, Ont. (this survey). Minnitaki Lake, Ont. (49°58′N, 92°00′W) Lac Seul, Ont. (50°20′N, 92°30′W) (both 1904, W. McInnes !). McCaulay Creek, 18 mi W of Atikokan, Ont. Small stream 3½ mi E of Finland, Ont. Old Woman Lake, 35 mi S of Kenora, Ont. (all this survey). Pond 31 mi W of Kenora, Ont. (1964, J. Cook !). Winnipeg River, 7 mi E of Seven Sisters Falls, Man. (1951, W. E. Godfrey !).

Brokenhead River system. Hazel Creek, 2 mi E of Hazel, Man. (this survey).

Red River system. Traverse Lake, S end, Brown's Valley, Minn. Traverse Lake, N end, 18 mi N of Brown's Valley, Minn. Red River, 2 mi NE of Drayton, N. D. Lower Red Lake, 1 mi S of outlets about 40 mi NNW of Bemidji, Minn. Rat River, 1½ mi S of La Rochelle, Man. La Salle River, Elie, Man. Seine River, 12 mi E of Winnipeg, Man. Cut Bank River 7 mi E of Mohall, N. D. (all this survey). Assiniboine River near mouth, Winnipeg, Man. (1964, I. Lubinsky !).

Lake Manitoba-Lake Winnipegosis drainage area. Lake Manitoba, east side, 1 mi N of Narrows (1964, M. Ouellet !). Lagoon at Ebb and Flow



Lake, 4 mi NNW of Kinosota, Man. (this survey).

Saskatchewan River system. Pond 8½ mi E of Kiscoty, Alta. (1962, F. R. Cook & C. B. Powell !). Shell River, 6 mi W of Prince Albert, Sask. Rocky Lake, 29 mi N of The Pas, Man. Root Lake, 19 mi N of The Pas, Man. (all this survey).

Nelson River system. Lake Winnipeg, SW corner, 20 mi S of Gimli, Man. O'Hanly River, 18 mi N of Pine Falls, Man. Stout Lake, at outlet, Ont. (52°08′N, 94°44′W) (all this survey). Playgreen Lake, Man. (54°00′N, 98° 10′W) (1878, R. Bell !). Burntwood River, Thompson, Man. (this survey).

Owl River system. Owl Lake, Man. (56°22′N, 94°35′W) (this survey).

Churchill River system. Flotten River, 20 mi N of Dorintosh, Sask. (1962, F. R. Cook and C. B. Powell !). Otter Rapids, Churchill River, 54 mi N of La Ronge, Sask. White Stone Lake, Man. (56°27′N, 97°30′W). Brochet Lake, Man. (58°35′N, 101°35′W). Opachuanau Lake, Man. (56°44′N, 99°37′W) (all this survey). Waskaiowaka Lake, Man. (56°30′N, 96°20′W) (1906, O. O'Sullivan !).

Mackenzie River system. Inlet of Horn Lake, 10 mi SW of Whitecourt, Alta. Athabasca River at mouth of Tawatinaw River, Alta. (both this survey). [Slave River], 25 mi W of Fort Smith, N. W. T. (1964, L. H. Walkinshaw !). Mouth of Hay River, N.W.T. (1919, E. J. Whittaker !). Beaver Lake, 30 mi SE of Fort Providence, N. W. T. (1921, E. J. Whittaker !). Little Lake [Mills Lake], Mackenzie River, N.W.T. (1917, E.M. Kindle !). "South Side of Little Lake" [Mills Lake] Mackenzie River, N.W.T. (1919, E.J. Whittaker !). Mackenzie River near Dory Point, N.W.T. Great Slave Lake, north end, opposite Rae, N.W.T. Prosperous Lake, near Yellowknife, N.W.T. Pools 7 mi W of Yellowknife. Yellowknife River, 7 mi N of Yellowknife (all 1966, R. W. Coleman !) Keller Lake, N.W.T. (63°59′N, 121°42′W) (1962, L. Johnson !). Fossil Lake, 8 mi N of Fort Good Hope, N.W.T. (66°17′N, 128°51′W) (1962, E. W. Innes !).

Distribution (of *Planorbula armigera* plus *P. jenksii* Carpenter; see "Remarks"): New Brunswick west to southeastern

Ontario, then west to Saskatchewan and northwest to the Mackenzie River system (at least to 66°N; NMC, records). According to Baker (1928a: 359) it is also distributed as far south as Georgia and Louisiana and west to Nebraska. Taylor's (1966: 89) statement that *Planorbula campestris* is the only *Planorbula* in the west does not apply to Canada.

Biology and Ecology: Although *Planorbula armigera* occurred at a large number of stations visited during this survey, it was rare or occasional at most of them. Living specimens were abundant at only 6 localities, viz.: in muskeg near Fort Albany and near Attawapiskat, Ont.; in sheltered, heavily vegetated coves in the north and south ends of Severn Lake, Ont.; in muskeg near Red Sucker Lake, Man.; and in a sluggish stream full of vegetation near Finland, Ont. At each of these localities it was, in fact, the dominant molluscan species. The first 5 localities are close to the northern edge of the range of this species in Ontario and northeastern Manitoba. *P. armigera* was particularly large and abundant in muskeg near Attawapiskat (as were some other gastropod species) and it may be that 1 huge population extends throughout the whole Hudson Bay Lowlands region.

Elsewhere *Planorbula armigera* occurred as a minor element of several rich gastropod faunas and under diverse ecological conditions. It always occurred in lentic or slow-moving lotic environments, however, and among vegetation. Baker (1928a: 358) considers it characteristic of " swales and of small and stagnant bodies of water."

The anatomy of this species has been admirably discussed by Baker (1928a: 356-8; 1945: 174-7). The living animal is blackish and quite active. The tentacles are long and filiform and the shell is carried at an angle of about 45°. According to Baker (loc.cit.) the radula formula varies from 18-1-18 to 24-1-24. A specimen from the southern end of Severn Lake, northern Ontario, with a diameter of 5·9 mm had a radula formula of

$$\frac{8}{4\text{-}6}-\frac{9}{3}-\frac{1}{2}-\frac{9}{3}-\frac{9}{4\text{-}5}\,(17\text{-}1\text{-}18).$$

Remarks: According to Pilsbry (1934: 54), *Planorbula armigera* and *P. jenksii* are distinct, the latter being distributed only in eastern North America. Pilsbry did not cite any distinguishing characters then or subsequently, however. Both "species" were recognized by Baker (1945: 174) even though Baker's own work failed to reveal significant anatomical or conchological differences between them. Robertson & Blakeslee (1948: 70) also assumed that the distinction was valid and listed all specimens from the Buffalo, New York area as *P. jenksii*. The separate status of these nominate species (and of *P. lautus* Adams, *P. crassilabris* Walker, and *P. armigera* var. *palustris* Baker) is questionable and remains to be evaluated after examination of representative collections from many parts of the North American range of the whole " *armigera-jenksii* complex. " Such material is not available to me and such a revision is also beyond the scope of this work, although evidence from the Canadian Interior Basin specimens and other material indicates that at least *P. palustris* is not distinct from *P. armigera* (*s. str.*). The distributions of both *P. armigera* and *P. jenksii* are considered together under " Distribution " above.

Planorbula campestris (Dawson)
Plate 13, Figs. 6-8; Map 80

Segmentina armigera var. *campestris* Dawson, 1875: *Report on the geology and resources of the region in the vicinity of the forty-ninth parallel,*

(etc.). Appendix E, p 349. Type locality: " Pointe du Chéne. Dufferin. Trader's Road. 500 Mile Lake. "

Segmentina (*Planorbula*) *christyi* Dall, 1905: *Land and fresh water mollusks of Alaska and adjoining regions*. Harriman Alaska Exped., *13*: 99. Type locality: " High Bluff, Manitoba [and] Fort Smith, Mackenzie River [Slave River]. "

Diagnosis: Shell planorbiform, medium-sized, whorls rounded, spire nearly flat, body whorl not bent downward near aperture, with 1 to 4 sets of 5 tooth-like processes present far inside the aperture in most juveniles but absent in fully grown adults.

Description: Shell medium-sized (up to about ½ inch in diameter), planorbiform, dextral, pale brown to dark brown, and with fine, close, silky incremental lines and fine, sharp, spiral striae. Whorls about 6 in full-grown individuals, rounded, and without carinae. Spire flat or slightly concave centrally. Umbilicus wide, deep, funnel-shaped and showing all whorls. Last part of body whorl very slightly expanded and in the same plane as, or slightly lower than, the penultimate whorl (but not sharply bent down as in *Planorbula armigera*). Lip thin. Aperture ovate to subquadrate, prosocline, and at an angle of about 25° to the umbilical axis. Within the aperture in juvenile specimens are up to 4 sets of denticles, each set with 5 tooth-like processes similar to those in *P. armigera* except that the small uppermost process seen in *P. armigera* (which has 6 processes) is absent in *P. campestris*. In full-grown specimens of *P. campestris* these " teeth " are not present.

Measurements:

Feature	N	Range	Mean	S.E $_M$	S.D.
Pond 4 mi N of Elk Point, Alta.					
Diameter, mm	13	5·7 —11·7	9·35	—	—
Height/Diameter	13	0·34— 0·44	0·372	0·008	0·028
Whorls	13	4·3 — 6·1	5·28	—	—
Pond, Lintlaw, Sask.					
Diameter, mm	20	8·2 —11·8	10·51	—	—
Height/Diameter	20	0·32— 0·37	0·346	0·003	0·013
Whorls	20	5·6 — 6·2	5·59	—	—
Pond near Usherville, Sask.					
Diameter, mm	7	6·2 —11·1	8·44	—	—
Height/Diameter	7	0·32— 0·38	0·354	0·008	0·022
Whorls	6	5·5 — 5·9	5·43	—	—

The largest specimen observed was from a pond 3 mi E of Parkbeg, Sask. It measured: diameter 12·3 mm, height 4·6 mm, whorls $6\frac{3}{10}$.

Records:

Winnipeg River system. Roadside ditch 6 mi W of Whitemouth, Man. (this survey).

Red River system. Assiniboine River drainage area: Pond 3 mi E of Parkbeg, Sask. (this survey). Pond, Moose Jaw, Sask. (1961, F. R. Cook and M. G. Foster !). Kelliher, Sask. (Mozley, 1938: 110). Creek 1 mi E of Indian Head, Sask. (this survey). Pond, Usherville, Sask. (1963, F. R. Cook and C. B. Powell !) Ponds in Moose Mountain Forest Reserve Sask. Wade's Slough, Beulah, Man. Birtle, Man. (all Mozley, 1938: 110). Small lake $4\frac{1}{2}$ mi W of Hamiota, Man. (1906, J. Macoun!). High Bluff, Man. (Dall, 1905: 99). Red River drainage area: Pond 4 mi SW of Winnipeg, Man. Pond near St. Vital, Man. (both Mozley, 1938: 130). Marsh, 9 mi W of Langdon, N. D. (this survey).

Devil's Lake drainage area. (Inland drainage). Mauvaise Coulée, ditch north of Lac aux Morts, and pond 2 mi W of " Garske " (all Winslow, 1921: 12-13).

Quill Lakes drainage area. (Inland drainage.) Pond 5 mi NW of Wadena (1962, F. R. Cook and C. B. Powell !). Wadena. Near Hudson Bay Lake, Touchwood (both Mozley, 1938:110).

Chin Coulée drainage area. (Inland drainage). 15 mi N of Stirling (1966, R. Hartland-Rowe !).

Lake Winnipegosis drainage area. Pond, Lintlaw, Sask. (1962, F.R. Cook & C. B. Powell !).

Saskatchewan River system. South Saskatchewan River drainage area: 10 mi. SE of Cardston, Alta. 6 mi W of Wrentham, Alta. 8 mi N of Waterton, Alta. Pond near Priddis, Alta. (all 1965, 1966, R. Hartland-Rowe !). Waskasoo Creek, 3 mi S of Penhold, Alta. Pond 2 mi NNW of Red Deer, Alta. (both this survey). North Saskatchewan River drainage area: Tofield, Viking and Phillips, Alta. (all Mozley, 1938: 110). Pond, 2 mi E of Poe, Alta. (this survey). Pond, 7 mi E of Spruce Grove, Alta. (1963, Joyce Cook!). Pond 1 mi E of Lindbrook, Alta. (this survey). 7 mi W of Stony Plain, Alta. (1963, Joyce Cook!). Ponds $\frac{1}{2}$ mi N of Salvador, Sask. Pond 14 mi N of Glaslyn, Sask. (both 1962, F. R. Cook and C. B. Powell !).

Churchill River system. Pond 1 mi S of Goodsoil, Sask. Pond 3 mi NW of Meadow Lake, Sask. (both 1962, F. R. Cook and C. B. Powell!).

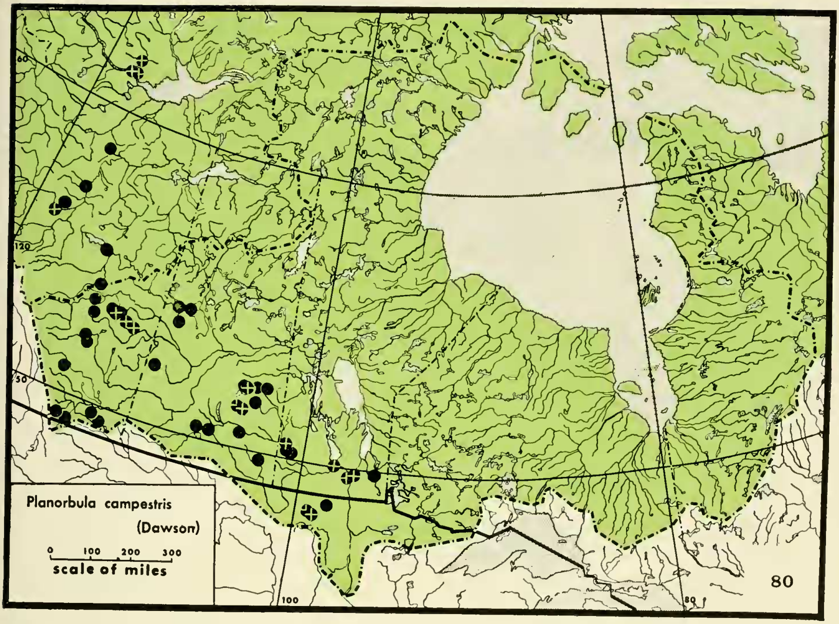
Mackenzie River system. Peace River drainage area: 3 mi N of Spirit River, Alta. (Mozley, 1938: 110). Swamp near Notikewin River bridge, [Manning], Alta. (1932, L.S. Russell !). 4 mi E of High Level, Alta. (1965, R. Hartland-Rowe!). Leith River [Little Burnt River], 2 mi NNW of Whitelaw, Alta. (this survey). Athabasca River drainage area: Lesser Slave Lake, Slave Lake, Alta. Tawatinaw River, 1 mi N of Rochester, Alta. (both this survey). Slave River drainage area: Fort Smith, Mackenzie River [sic!, Slave River, N.W.T.] (Dall, 1905: 99; Miller, 1968: 262). Mackenzie River drainage area: Mackenzie River and vicinity near Great Slave Lake (4 localities) (Whittaker, 1924: 9, 11).

Distribution: Southern Manitoba and North Dakota, south to Utah and New Mexico, west to British Columbia, and north at least to 60°N in the Mackenzie River system.

Planorbula campestris has also been recorded from southwestern Ontario (Miller, 1968: 262). This locality (Belleville, Ont.) is more than 1,000 miles east of all other known localities for *P. campestris*. It is probably caused by a confusion of data; the record is almost certainly incorrect.

Biology and Ecology: Among the 10 lots of living specimens collected during this survey, 3 lots are from swamps; 1 from a temporarily flooded area near a large lake; 1 from a roadside ditch; 1 from a swampy, slow-flowing stream about 10 feet wide; and 4 from ponds between $\frac{1}{2}$ and 2 acres in area. In June when collections were made these ponds appeared to be permanent, although this is uncertain. Mozley (1938: 111) describes their habitat as " temporary ponds rarely in permanent ponds which have a temporarily flooded area around them ." In all 10 localities cited above the bottom was of mud and at 9 of the localities aquatic vegetation was dense. Associated species frequently included *Lymnaea elodes*, *Promenetus exacuous exacuous*, and *Gyraulus parvus*.

No detailed study of the anatomy of this species has been made. The soft parts are in general blackish but paler on the long, narrow tentacles and on the bottom of the foot. The radula formula



of a specimen (diameter 7·6 mm) from a creek 1 mi E of Indian Head, Sask. is $\frac{12}{4\text{–}7}-\frac{11}{3}-\frac{1}{2}-\frac{11}{3}-\frac{12}{4\text{–}7}$ (23-1-23).

Remarks: The tooth-like processes inside of the aperture characteristic of *Planorbula* are present only in juvenile *P. campestris.* Among the material examined, most specimens with diameters smaller than $4\frac{1}{2}$ mm possess from 1 to 4 successive sets of denticles. Most specimens larger than this have no tooth-like processes at all, but a few have been observed with diameters of $4\frac{1}{2}$ to 7 mm which still retain multiple sets. The observation that *P. campestris* may have multiple sets of denticles has been made independently by Miller (1968: 256) who discusses this phenomenon and cites specimens up to 9·6 mm diameter with 2 sets of denticles.

Genus *Helisoma* Swainson

Helisoma Swainson, 1840: *A Treatise on Malacology*, p 337. Type, by original designation, " *H. bicarinata* Sow. Gen. f. 4 " [=*Planorbis bicarinatus* Sowerby, 1821; =*P. bicarinatus* Say, 1817, (preoccupied); =*P. anceps* Menke, 1830].

Shells medium-sized to large, planorboid, dextral or sinistral, relatively high, of comparatively few whorls, carinate or acarinate, striate or smooth and with the spire depressed or elevated. Growth in this genus is allometric; young specimens are proportionately very much higher than adults.

Baker (1945: 123-154) and Hubendick (1955: 483-487) have described in detail the internal morphology of many species of *Helisoma*. The genus is characterized by the possession of a fan-shaped prostate, an external penial gland duct, and by having only 1 retractor muscle in the penial

PLATE 26. Planorbidae (II)

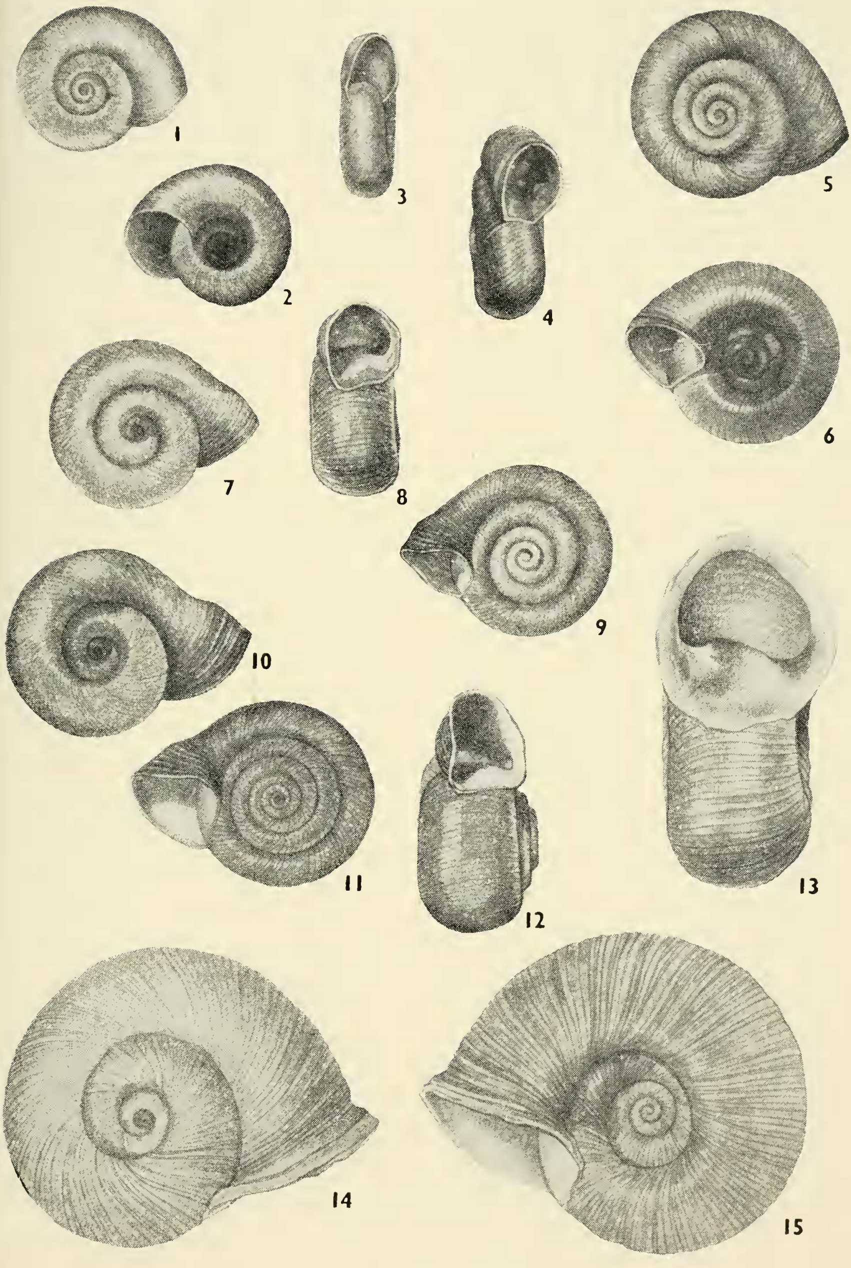
FIGS. 1–3. *Promenetus umbilicatellus* (syntype), bear Brandon, Manitoba (USNM 63390, 5·0 mm). . . . . p 415

FIGS. 4–6. *Planorbula armigera*, Kenogamisis Lake, near Geraldton, Ontario (NMC 19314, 6·7 mm). . . . . p 419

FIGS. 7–9. *Helisoma campanulatum campanulatum*, Lac Dubuisson near Val d'Or, Quebec (NMC (NMC 19049, 12 mm). . . . . p 445

FIGS. 10–12. *Helisoma campanulatum collinsi*, Wabaskang Lake, 40 mi N of Vermilion Bay, Ontario (NMC 19308, 14 mm). . . . . p 451

FIGS. 13–15. *Helisoma trivolvis subcrenatum*, Third Vermilion Lake, Banff, Alberta (NMC 29747, 25 mm). . . . . p 456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complex. *Helisoma* now occurs in the Western Hemisphere only (1 Pleistocene species is recorded from northeastern Asia) and fossil *Helisoma* are known from deposits as old as Pliocene.

Helisoma, as here considered (in part following Baker, 1945 and Zilch, 1959: 129), contains *Pierosoma* Dall, *Planorbella* Haldeman, *Seminolina* Pilsbry, and *Helisoma* (*s. str.*) as subgenera.

Based on direction of coiling and on shell form Taylor (1966: 111, 131) has raised *Planorbella* to generic rank, with *Pierosoma* Dall and *Seminolina* Pilsbry as contained subgenera. Anatomical characters partly substantiate this new grouping (see Baker, loc. cit. and Hubendick, loc. cit.), although anatomy also shows that *Helisoma*, in the traditional sense, is a natural interrelated group.

Within any large genus the contained subgenera may be separated by unequal morphological gaps. In such cases it may be undesirable to regroup more closely related subgenera into new genera unless important, phylogenetically significant characters indicate a clear necessity to do so. None of the characters that support the proposed regrouping appear to be in this category. Furthermore, this revision, if accepted, would make mandatory the use of *Planorbella* instead of *Helisoma* for most of the species now known as *Helisoma*. *Helisoma* is so firmly established in the literature of malacology, limnology, and parasitology that it should be preserved in its established sense unless compelling reasons demand otherwise. *Helisoma* is therefore retained and broadly applied in this work.

Subgenus *Helisoma* (*s. str.*)

Shells medium-sized, dextral, hyperstrophic, of few whorls, strongly carinate above and below (in most populations), spire depressed, umbilicus funicular and aperture expanded and slightly thickened.

The anatomy of *Helisoma* (*s. str.*) is discussed in detail by Baker (1945: 124-129). *Helisoma* (*s. str.*) differs from other subgenera within the genus in the morphology of the genitalia (see Baker, loc. cit.) and in several, rather striking shell characters. It is a North American group occurring from Mexico to the subarctic. Two species and numerous subspecies have been recognized, several of which are synonymized here. Geologic range: Miocene (?), Pliocene to Recent.

Helisoma (*Helisoma*) *anceps anceps* (Menke)

Plate 14, Figs. 1-3; Map 81.

Planorbis bicarinatus Say, 1817: *Nicholson's Encyclopedia*, 1st Amer. ed., pl. 1, fig. 4 (Binney reprint, 1858: 44, pl. 69: 4). Type locality not specified but presumably near Philadelphia. Not *Planorbis bicarinatus* Lamarck, 1804.

Planorbis anceps Menke, 1830: *Molluscorum....* in *Museo Menkeano* (*etc.*). p 36. No description but refers to " Lister Conch. tab. 139. fig. 44." Type locality given by Martini Lister (1770) is " virgin [ia] ". See " Remarks on the identity of *Planorbis anceps* Menke " below.

Planorbis antrosus Conrad, 1834: *Amer. J. Sci.*, (1) *25* : 343. Type locality: " Randon's Creek, near Claiborne, Alabama, adhering to Limestone rocks. "

Diagnosis: Shell medium to large, planorboid, relatively high, spire immersed, collabral sculpture fine, and in most specimens carinate on the upper surface of the body whorl and near the umbilicus.

Description: Shell medium-sized to large (up to about 17 mm in diameter), planorbiform, with about 4 whorls, ultradextral, variable, relatively high, blackish brown to pale brown, and in most populations with 2 prominent carinae, 1 on the upper surface of the body whorl and 1 bounding the umbilicus. Upper and lower carinae (when present) rounded, sharp, or corded; the upper carina of variable position and

located at the centre of the whorl or close to, but not on, the shoulder. Periphery rounded. Spire immersed to a variable extent but in most populations it is deeply recessed. Umbilicus deep and narrow. Spiral striae absent or present and of prominence varying from barely apparent to strong and obvious. Collabral sculpture present and fine to moderately fine. Aperture ear-shaped, expanded in some populations, commonly thickened internally, and with a moderately thick callus deposit on the parietal wall.

Measurements:

See text fig. 9 and " Remarks " for explanation of abbreviations and further measurements; also see Charts 27 to 33 (populations 1–10, 16–22).

Feature	N	Range	Mean	S.E.$_M$	S.D.
Cave and Basin Spring, Banff, Alta.					
Max. Dia., mm	13	7·0 —10·8	9·14	—	—
Gr. Dia., mm	13	7·0 — 9·9	8·43	—	—
Height, mm	13	4·1 — 6·0	5·02	—	—
Umbil. Dia., mm	13	3·1 — 5·0	4·0	—	—
Umbil. Dia./Gr. Dia.	13	0·43 — 0·54	0·475	0·009	0·033
Whorls	13	3·4 — 3·8	3·60	—	—
Montreal Lake, 16 mi N of Waskesiu Lake, Sask.					
Max. Dia., mm	30	6·6 —15·0	12·3	—	—
Gr. Dia., mm	30	6·6 —15·0	11·4	—	—
Height, mm	30	4·3 — 8·7	6·99	—	—
Umbil. Dia., mm	30	3·3 — 7·1	5·55	—	—
Umbil. Dia./Gr. Dia.	30	0·40 — 0·54	0·475	0·007	0·036
Whorls	30	3·3 — 4·5	3·99	—	—
Sand Lake, 8 mi N of Virginia, Minn.					
Max. Dia., mm	29	7·2 —12·2	9·93	—	—
Gr. Dia., mm	29	7·2 —11·9	9·28	—	—
Height, mm	29	4·3 — 6·5	5·38	—	—
Umbil. Dia., mm	29	3·4 — 6·0	4·32	—	—
Umbil. Dia./Gr. Dia.	29	0·41 — 0·53	0·465	0·006	0·033
Whorls	29	3·1 — 4·1	3·63	—	—

Records:

Because of uncertainty regarding subspecific evaluations by previous workers, most literature records from the area as here defined are omitted from the following list. For records not listed here see Mozley (1938).

Eastmain River system. Eastmain River, Eastmain, Que.

Rupert River system. Rupert River, 46 mi W of Lake Mistassini, Que. (NMC, collector?). Bordeleau River, near Baie Spawning, Lac Waconichi, 20 mi NE of Chibougamau, Que. (this survey).

Nottaway River system. Small stream 4 mi N of Louvicourt, Que. Small river 9 mi NE of Demaraisville, Que. Waswanipi River, 22 mi NE of Demaraisville (all this survey).

Moose River system. Abitibi River, 17 mi N of Cochrane, Ont. Pond 6 mi S of Matheson, Ont. Black River, Matheson. Nellie Lake, Nellie Lake, Ont. Inlet of Remi Lake, 14 mi E of Kapuskasing, Ont. Kwataboahegan River mouth, 12 mi SW of Moosonee, Ont. Moose River, 8-10 mi S of Moosonee, Ont. Moose River, Moosonee and Moose Factory, Ont. (all this survey). Shipsands Island, mouth of Moose River (1933, H. G. Richards !).

Albany River system. Nagagamisis Lake, 20 mi N of Hornepayne, Ont. Skunk River, 38 mi W of Hearst, Ont. Nagagami River, 40 mi W of Hearst. Pagwachuan River, 70 mi W of Hearst. Klotz Lake, 30 mi E of Longlac. Lydia Lake, 23 mi E of Longlac, Long Lake, Longlac. Small lake 3 mi N of Geraldton. Hanover Lake, 24 mi NW of Nakina, Ont. (*anceps-royalense* intergrades). Elongate lake, 20 mi E of Beardmore, Ont. (*anceps-royalense* intergrades). Pools near Albany River, Fort Albany, Ont. St. Ann's Lake, Sinclair Island, Fort Albany (strongly striate) (all this survey).

Attawapiskat River system. Small stream 4 mi W of Pickle Crow, Ont. Attawapiskat River, 6 mi W of Attawapiskat, Ont. (both this survey).

Winisk River system. Winisk River, 15 mi S of Winisk, Ont. (this survey).

Hayes River system. Red Sucker Lake, west end, Man. (54°10′N, 93°57′W). Knee Lake at northern narrows (55°04′N, 94°45′W) and near outlet (55°10′N, 94°25′W), Man. (all this survey).

Winnipeg River system. Paguchi Lake, 7 mi N of Ignace, Ont. Nugget Creek, 12 mi E of Dryden, Ont. Chadwick Lake, 15 mi E of Kenora, Ont. Sand Lake, 8 mi N of Virginia, Minn. ("*unicarinata*" morph). Lake 12 mi S of Sioux Narrows, Ont. (all this survey). Sturgeon Lake, Rainy River District, Ont. (1929, A. R. Cahn!). Little Pine Lake, Finland, Ont. Lake of the Woods, Kenora, Ont. Moth Lake, 25 mi W of Kenora. Falcon Lake, Falcon Lake, Man. (all this survey). Pond 3 mi E of Falcon Lake (1962, F. R. Cook and C. B. Powell!). Roadside ditch 10 mi W of Falcon Lake. Whitemouth River near Whitemouth, Man. (both this survey).

Red River system. Red River drainage area: Red River, Abercrombie, N. D. Lower Red Lake, 1 mi S of outlet into Red Lake River, Minn. Rat River, 50 mi SSE of Winnipeg, Man. Seine River, near Winnipeg, Man. (all this survey). Assiniboine River drainage area: Whitesand River, 9 mi ESE of Shehc, Sask. Clear Lake, N shore, 8 mi N of Wasagaming, Man. Rolling River, 8 mi NW of Erickson, Man. Creek 8 mi ENE of Erickson, Man. Minnedosa River, 11 mi NNE of Elphinstone, Man. (all this survey).

Lake Manitoba-Lake Winnipegosis drainage area: Barrier Lake and Kipabiskau Lake (both 1964, D. Delorme !). Red Deer River mouth, Man. (all this survey). Lake Manitoba, east side, at the following localities : 1 mi N of narrows, 7 mi N of Moosehorn, and 7 mi W of Ashern. Lake Winnipegosis, Denbeigh Point (2 localities) (all 1964, M. Ouellet !).

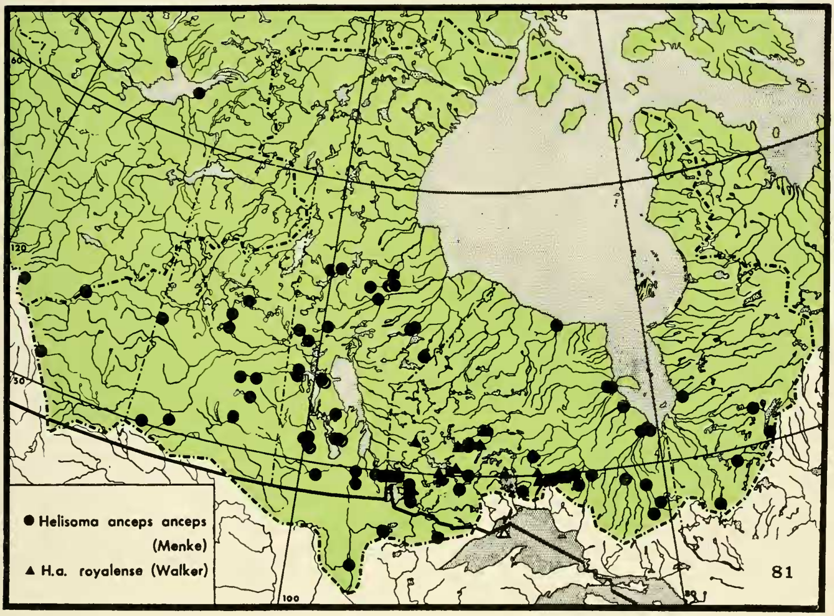
Saskatchewan River system. South Saskatchewan River drainage area: Cave and Basin Spring, Banff, Alta. (1915, E. M. Kindle !; also this survey). Red Deer River at mouth of Blindman River, Alta. (1927, R. L. Rutherford!). Swift Current Creek, 3 mi N of Waldeck, Sask. Creek, Piapot, Sask. South Saskatchewan River, 2 mi S of Outlook, Sask. (all this survey). North Saskatchewan River drainage area: Seba Beach, Lake Wabamun, Alta. (1926, L. S. Russell !). Englishman River, 3 mi N of Spruce Lake, Sask. (this survey). Saskatchewan River drainage area: Cormorant Lake, Man. (collector ?). Lake NW of Cormorant Lake, Man. Wekusko Lake (54°45′N, 99°50′W) Man. (both 1906, W. McInnes!).

Nelson River system. West shore of Lake St. Martin, 3 mi SE of Gypsumville, Man. (1964, M. Ouellet!). Burntwood River, Man. (1906, W. McInnes!). Limestone Lake (56°35′N 96° 00′W), Man. (this survey).

Churchill River system. Montreal Lake, 16 mi N of Waskesiu, Sask. Montreal River, 1 mi N of Montreal Lake (both this survey). Lac la Ronge, La Ronge, Sask. (whitefish stomachs) (1954 Univ. Sask.!). Eden Lake (56°38′N, 100°15′W), Man. Opachuanau Lake (56°44′N, 99°37′W), Man. White Stone Lake (56°27′N, 97°30′W), Man. Recluse Lake, Little Churchill River (56°55′N, 95°45′W), Man. (all this survey).

Athabasca River system. Pyramid Lake, Jasper National Park Alta. (Mozley, 1938: 105). Madeline Lake (62°33′N, 114°05′W), N.W.T. (1966, R. W. Coleman!).

Distribution: *Helisoma anceps* (*s. lat.*) occurs throughout North America from southern James Bay and Hudson Bay south to North Carolina, Alabama,



Texas, and northwestern Mexico and west to Oregon, Alberta (Walker, 1909: 24-28, Hibbard & Taylor, 1960: 103), and southwestern Northwest Territories (this survey). It has also been found in South Carolina and in Georgia by H. D. Athearn (pers. comm., Sept., 9, 1967) and in Italy by Henrard (1968) where it has been recently introduced. The nominate subspecies extends at least from the Potomac River system in Virginia (the type area) to the Canadian Interior Basin in Canada. In the latter region it is found from Quebec to Alberta and Great Slave Lake. The limits of its distribution south of Canada remain to be established when the status of the several nominate " subspecies " in the United States, and their ranges, become known.

Biology and Ecology: During this survey *Helisoma anceps* was found in several kinds of permanent aquatic habitats but not in temporary ones. Seventy lots were collected. Of these 21 are from large lakes, 9 are from small lakes, 2 are from permanent ponds, 3 are from backwaters, and 1 is from a canal. Among lotic environments 14 lots are from rivers over 100 feet in width, 7 are from rivers of 50 to 100 feet wide, 6 are from rivers 25 to 50 feet wide, 6 are from rivers 10 to 25 feet wide, and 1 is from a warm brook 3 to 5 feet wide (the outlet of Cave and Basin Spring, Banff, Alberta). Bottoms were of all types and vegetation was present in various amounts at all localities where living specimens were taken. In lotic environments current varied from rapid to imperceptible. Mozley (1938: 105) states that this species (as *H. a. sayi*) occurs " usually in small streams or those of moderate size. " Baker

(1928a: 319-327) correlates several "varieties" with specific kinds of water bodies. See "Remarks."

Gastropods frequently co-existing with *Helisoma anceps* are *Physa gyrina*, *Amnicola limosa*, *Valvata tricarinata*, and numerous other species.

The anatomy of *Helisoma anceps* has been discussed in detail by Baker (1928a: 318; 1945: 124). The soft parts of the living animal are yellowish or brownish and spotted especially near the eyes. The tentacles are long and filiform and the shell is carried almost perpendicularly.

The radula formula, according to Baker (1945: 127), varies from 22-1-22 to 30-1-30. Specimens examined during the present work gave the following results:

Cat. No.	Locality	Max. Dia., mm	Radula Formula
29141	Winisk River near Winisk, Ont.	8·6	$\frac{15}{4\text{–}5}-\frac{6}{3}-\frac{1}{2}-\frac{6}{3}-\frac{14}{4\text{–}5}$ (21–1–20)
32232	Rolling River near Erickson, Man.	10·3	$\frac{17}{4}-\frac{6}{3}-\frac{1}{2}-\frac{6}{3}-\frac{18}{4}$ (23–1–24)
29007	Swift Current Creek near Waldeck, Sask.	10·8	$\frac{16}{4\text{–}5}-\frac{6}{3}-\frac{1}{2}-\frac{6}{3}-\frac{17}{4\text{–}5}$ (22–1–23)

Remarks on the Identity of *Planorbis anceps*: As mentioned in the synonymy above, Menke (1830: 36) gave no description of his *Planorbis anceps* but referred only to a figure ("tab. 139, fig. 44") in Lister's "Conch", presumably the second edition (1770) of Historiae Sive Synopsis Methodicae Conchyliorum [etc.] by Martini Lister. The figure in question is an umbilical view, in natural size (7·8 mm maximum diameter) of a shell which in my opinion is recognizable as the same species now called *Helisoma anceps* (Menke). It is not recognizable to subspecies, however, and the locality "virgin" [Virginia] is not sufficiently precise to solve the problem.

The 1st edition of Lister's work (in which the figure first appeared) was published in sections from 1685 to 1697. The specimen on which "tab. 139, fig. 44" was based is not in the British Museum (Wilkins, 1953; also personal communication from Mr. Norman Tebble, June 7, 1966) and must be considered to be lost. In 1685 the center of population in Virginia was at Williamsburg and although other settlements existed it is quite probable that the specimen came from eastern Virginia.

Some firm standard of reference for *Helisoma anceps* (*s. str.*) should be available for comparison in order that the subspecific status of other populations can be decided. Sufficiently large and unbiased population samples from the vicinity of Williamsburg are presently unavailable, however, and the selection of a neotype lot must be deferred until adequate material is at hand. A specimen closely resembling Lister's illustration has been figured by

Baker (1945, pl. 82, figs. 1, 2). That specimen is from Ashland, Virginia, about 50 miles from Williamsburg, and appears to represent the most widespread and abundant morphological subspecies in the eastern and central portions of Canada and the United States. A thorough investigation of *H. anceps* populations and selection of a neotype population should be made.

Remarks on measurements: Twelve "subspecies" of *Helisoma anceps*, in addition to the nominate subspecies, have been recorded from Canada. These are : *H. a. anticostianum* Baker, 1945; *H. a. aroostookense* Pilsbry, 1895; *H. a. cahni* Baker, 1928; *H. a. latchfordi* Pilsbry, 1927; *H. a. percarinatum* Walker, 1909; *H. a. politum* Baker, 1945; *H. a. portagense* Baker, 1908; *H. a. royalense* Walker, 1909; *H. a. rushi* Baker, 1939; *H. a. sayi* Baker, 1928; *H. a. striatum* Baker, 1902; and *H. a. unicarinatum* Haldeman, 1844. In order to identify the material collected and to evaluate in part the distinctness of these "subspecies" in the research area it was necessary to consider all distinguishing characters used by previous authors and to measure the inter- and intra-population variation of each character in the material available.

Twenty-one population samples were used for analysis including, for comparison, a lot from eastern Virginia. These are listed in Table 8 together with their maximum diameters (range and mean) and the number of specimens in each lot. The 20 largest lots were selected that would give the best geographical coverage of that part of the research area in which *Helisoma anceps* occurs.

The shell characters recognized as significant by Baker, Walker, and Pilsbry in defining subspecies within *Helisoma anceps* are (1) maximum diameter, (2) greater diameter, (3) relative height, (4) the ratio of umbilical diameter to greater diameter, (5) strength of the upper carina, (6) strength of the lower carina, (7) relative position of the upper carina, (8) strength of spiral striae, and (9) relative depression of the apex. The population samples listed were analyzed in detail for each of these characters. The results were then compared with ecological parameters and were mapped in an effort to expose correlations between morphology and ecology or geography.

Characters 1-6 were found to show much intra- and inter-population variation but variation of an erratic nature which could not be related to ecology or geography. Those results are therefore omitted from the following discussion. (These data are on file at the National Museum of Natural Sciences, National Museums of Canada, and are available to interested investigators.) Relative height was analyzed in detail and was found to change with growth, principally because juveniles grow more rapidly in relative height than do post-juveniles. The ratio H-1/Gr. Dia. was therefore more reliable than H/Gr. Dia. for comparing lots of mixed age classes, but even this could not be correlated with ecology or geography.

The 3 characters which were found to be useful are described below:

(A) Position of upper carina: A scored character evaluated by using standard reference specimens as follows: (1) carina at shoulder of body whorl, (2) carina located halfway between shoulder and middle of upper surface of body whorl, (3) carina located at middle of upper surface of body whorl.

(B) Spiral striation: Scored by use of standard reference specimens as follows: (1) spiral striation absent, (2) faint, (3) strong, (4) very prominent.

TABLE 8. Populations of *Helisoma anceps* analyzed statistically.

Population Number	Location	N	Maximum Diameter mm Min. (Mean) Max.
1	Cave and Basin Spring, Banff, Alta.	13	7·0–(9·1)–10·8
2	Seba Beach, Lake Wabamun, Alta.	5	8·6–(11·5)–13·0
3	Englishman River near Spruce Lake, Sask.	5	9·5–(11·0)–16·0
4	Swift Current Creek near Waldeck, Sask.	8	9·6–(10·4)–11·4
5	Montreal Lake near Waskesiu Lake, Sask.	30	6·6–(12·3)–15·0
6	Kipabiskau Lake, Sask.	9	10·0–(12·0)–14·2
7	Cormorant Lake, Man.	6	3·8–(11·3)–14·6
8	Clear Lake, Man.	27	8·2–(13·4)–16·5
9	Campbell Lake outlet near Erickson, Man.	13	9·7–(11·7)–13·9
10	Sand Lake near Virginia, Minn.	29	7·2–(9·9)–12·2
11	Chukuni River near Red Lake, Ont.	8	9·2–(11·5)–13·0
12	Abram Lake, Sioux Lookout, Ont.	30	4·6–(8·9)–13·4
13	Bamaji Lake, Ont.	6	11·8–(12·7)–13·9
14	Small stream near Pickle Crow, Ont.	11	11·9–(14·0)–16·9
15	Kenogamisis Lake near Geraldton, Ont.	30	5·1–(12·5)–16·9
16	Pond near Matheson, Ont.	8	6·7–(9·7)–12·2
	Northern peripheral populations		
17	Limestone Lake (56°35′N 96°00′W). Man.	8	10·0–(12·2)–14·3
18	Recluse Lake (56°55′N, 95°45′W), Man.	5	7·5–(11·1)–12·7
19	Knee Lake (55°04′N, 94°45′W), Man.	30	12·2–(13·2)–16·0
20	Kwataboahegan River mouth near Moosonce, Ont.	5	5·5–(11·5)–15·0
	Lot from *P. anceps* type area		
21	Roach's Run, Alexandria Co., Virginia.	8	8·1–(9·4)–10·8

(C) Apical depression: Scored by use of standards as follows: (1) apex very little depressed, upper surface nearly flat, (2) apex moderately depressed, (3) apex deeply depressed, i.e., as deep as the umbilicus.

Results: The most clear-cut geographical trend relates to the position of the upper carina (Chart 29). Population samples 11 to 15, and particularly 11, 12, and 15, all in western Ontario, show lower values than all other populations in the main west to east sequence, i.e., the upper carina is located more consistently on or close to the shoulder than in any other lots. This group is very easily distinguished by inspection of the specimens and differs from other population groups also in having lower values for apical depression scores (Chart 33). These populations represent *Helisoma anceps royalense* (discussed in following pages) and they form the only clearly differentiated subspecies of *H. anceps*

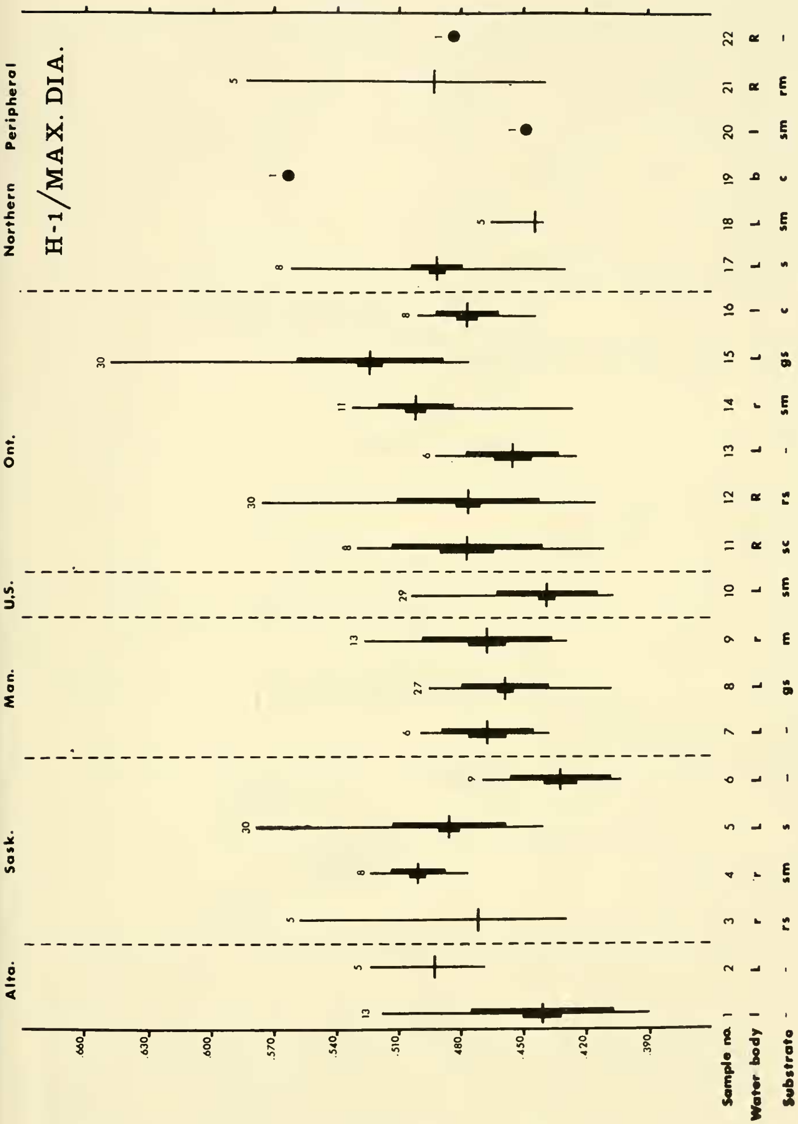


CHART 27. *Helisoma anceps* populations. For explanation see p 433. Symbols are defined in caption for Chart 1.

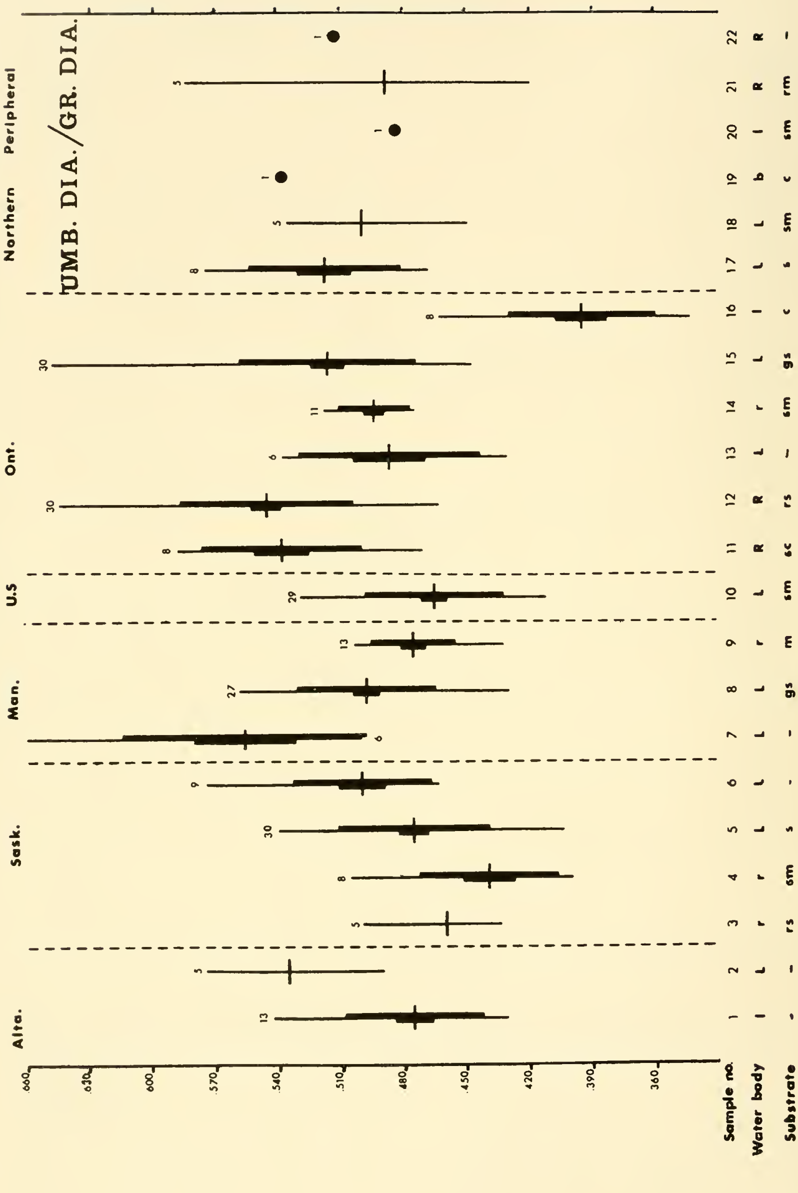


CHART 28. *Helisoma anceps* populations. For explanation see p 433. Symbols are defined in caption for Chart 1.

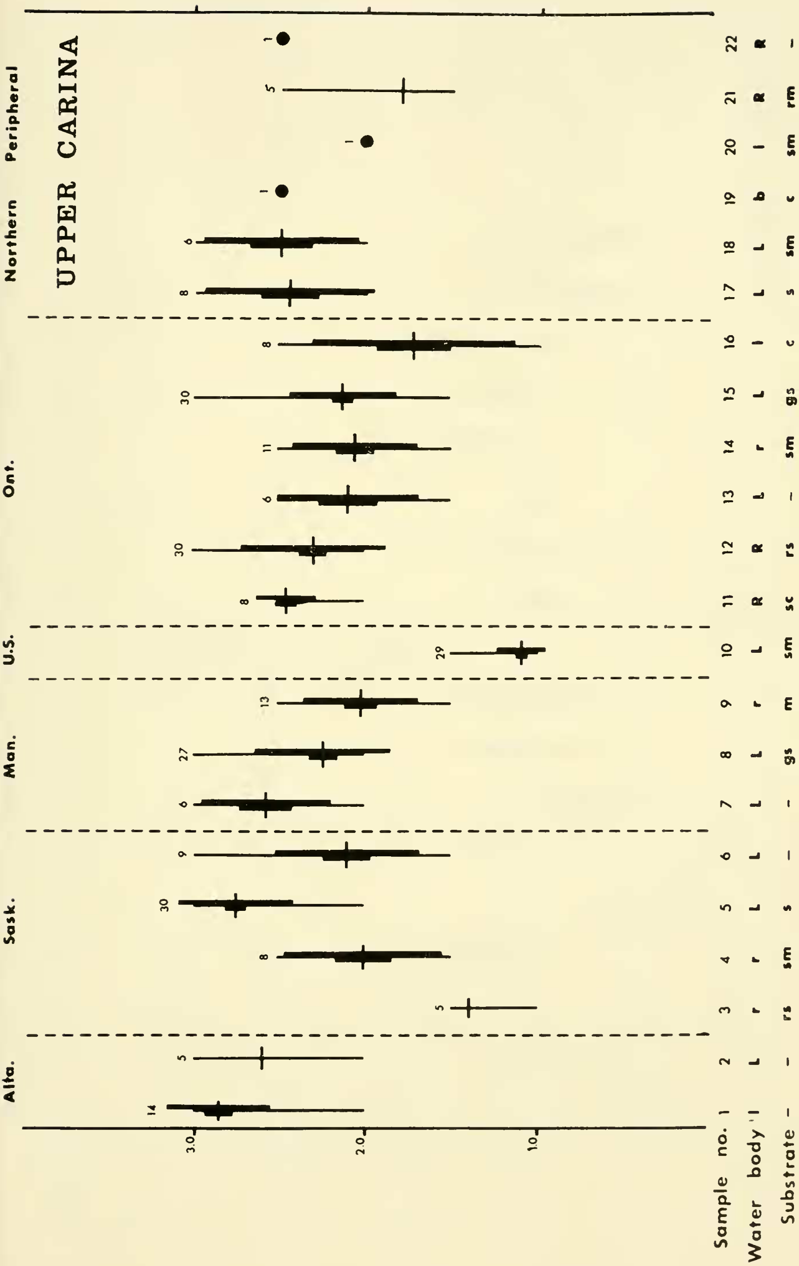


CHART 29. *Helisoma anceps* populations. For explanation see p 433. Symbols are defined in caption for Chart 1.

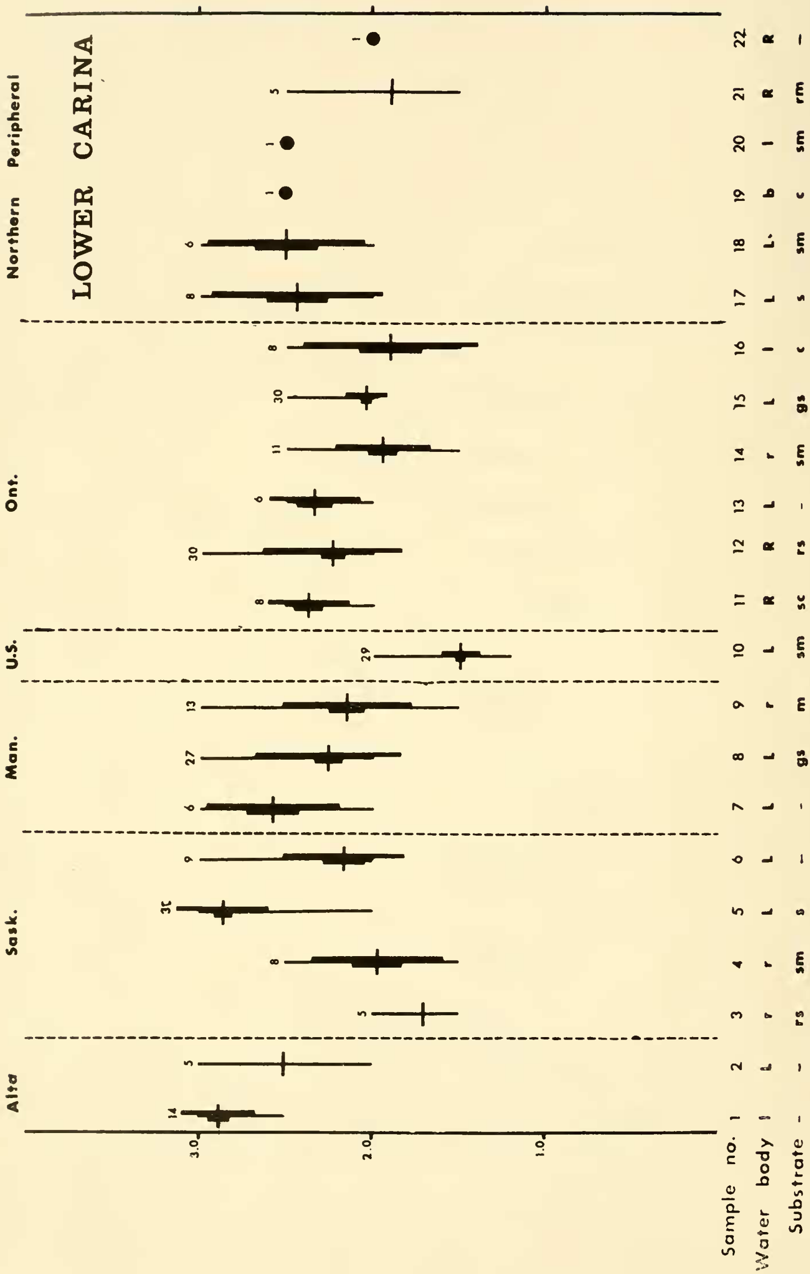


CHART 30. *Helisoma anceps* populations. For explanation see p 433. Symbols are defined in caption for Chart 1.

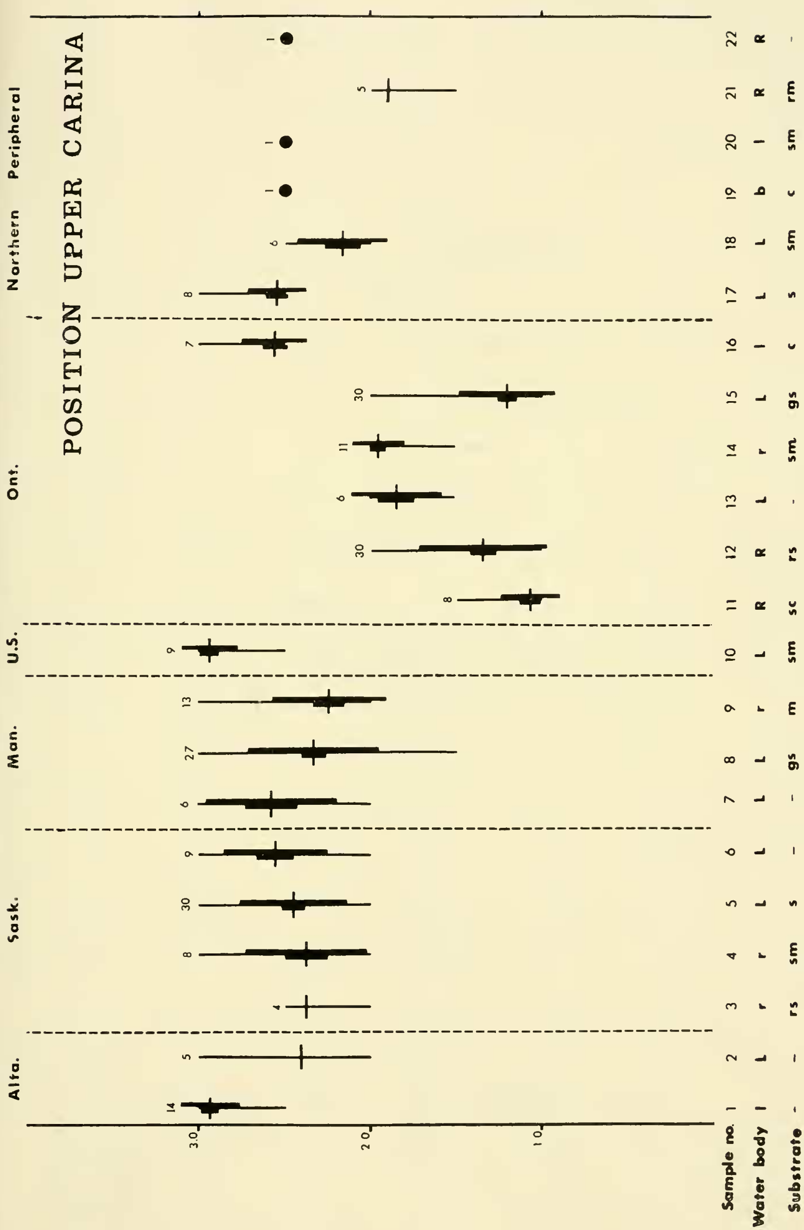


CHART 31. *Helisoma anceps* populations. For explanation see p 433. Symbols are defined in caption for Chart 1.

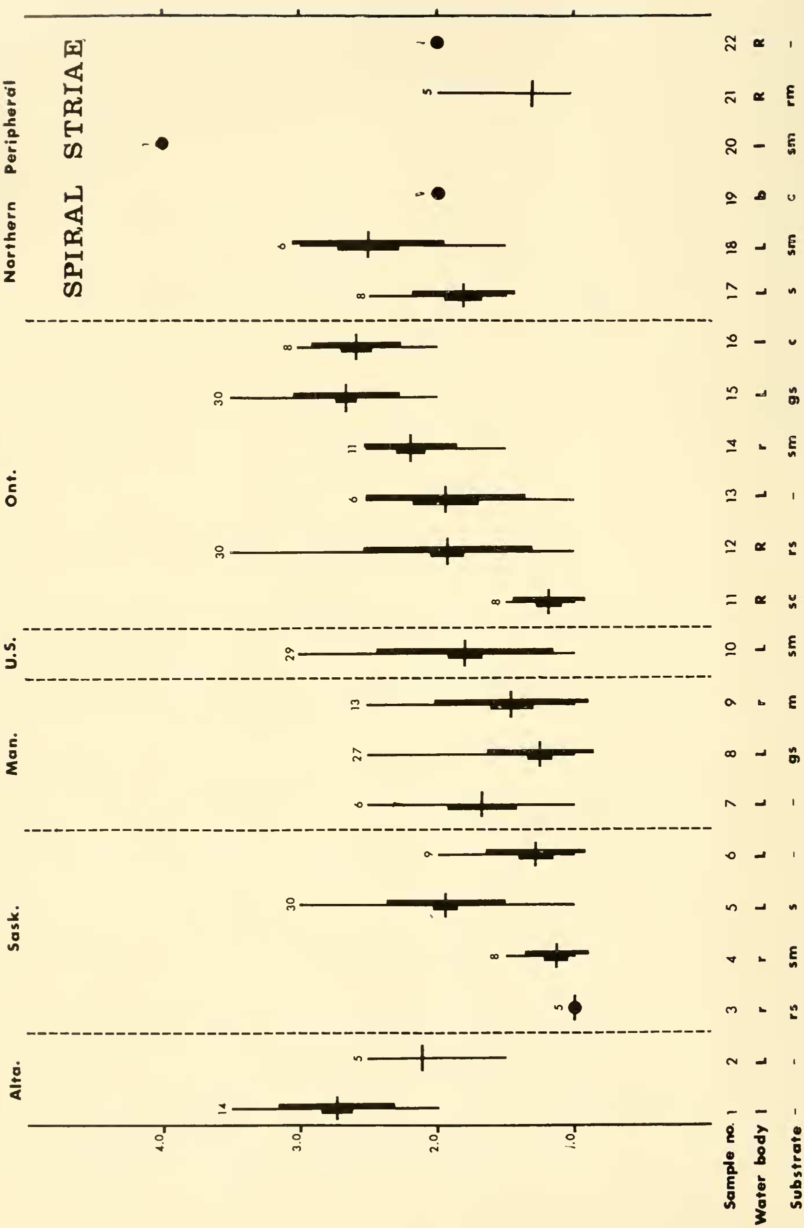


CHART 32. *Helisoma anceps* populations. For explanation see p 433. Symbols are defined in caption for Chart 1.

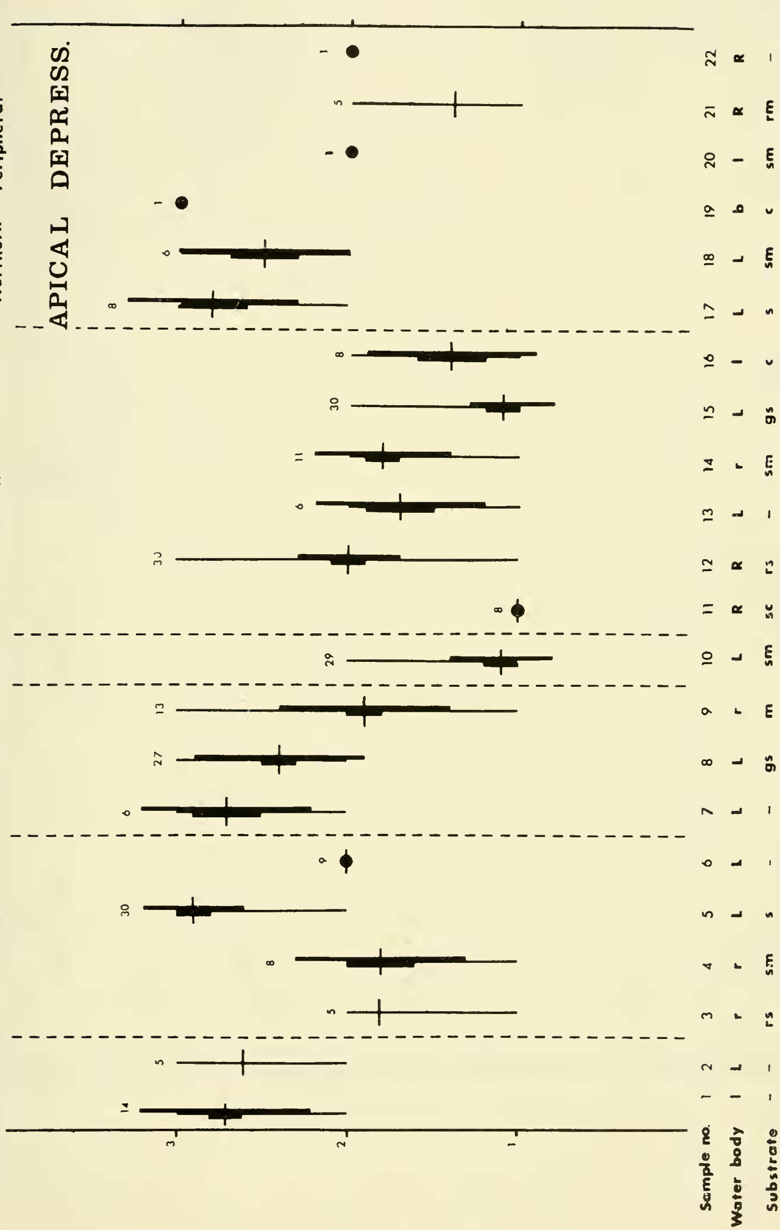


CHART 33. *Helisoma anceps* populations. For explanation see p 433. Symbols are defined in caption for Chart 1.

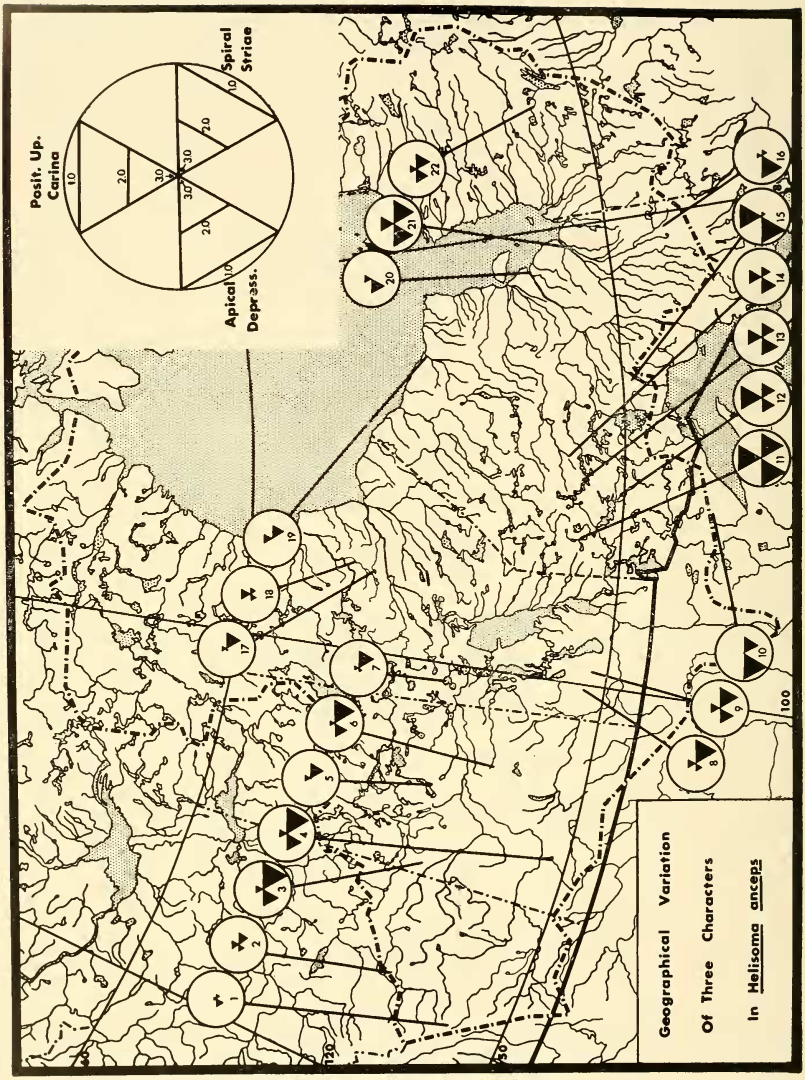


CHART 34. *Helisoma anceps* populations. For explanation see p 443.

in the region. Sample 21 also appears to be related to *H. a. royalense*; see " Remarks " under that subspecies.

Spiral striae are quite apparent in many populations. Striae are visible in some specimens of all populations except for sample 5 from Montreal Lake in northern Saskatchewan. The most strongly striate specimen seen is from St. Ann's Lake, Fort Albany, Ont. This supports the trend noticed by previous authors (e.g., Baker, 1928a) that northern populations tend to be striate. The nature of the shift from non-striate to striate populations is unclear from present material but the majority of the most striate lots are from Ontario or from northern peripheral localities (Chart 32). The degree of concordance existing between (*a*) upper carina position, (*b*) apical depression, and (*c*) spiral striation is shown on Chart 34.

Other characters which have been used to define subspecies are irregularly expressed and do not allow the delimitation of additional geographical subspecies. It is probable that most of the " subspecies " currently recognized are not geographically distinct and are taxonomically invalid but firm decisions on this must be deferred until analysis of more populations, including topotype populations, can be made.

Helisoma (*Helisoma*) *anceps royalense* (Walker)

Plate 25, Figs. 20-22; Map 81.

Planorbis bicarinatus var. *royalensis* Walker, 1909: *Nautilus*, *23*(1): 9. Type locality: " Siskowit Lake, Isle Royale, Lake Superior, Michigan. "
Helisoma anceps rushi F. C. Baker, 1939: *Can. J. Res.*, *17* (sec. D) (4): 94, fig. 1. Type locality: " Toad Island, Georgian Bay, Ontario. "

Diagnosis: Differing from *Helisoma anceps anceps* by having the upper carina prominent and at the shoulder of the body whorl; by having a shallower, flatter spire depression and flatter sides, and by the presence of coarser, heavier collabral sculpture.

Description: As diagnosed above. The upper carina is the chief diagnostic feature of this subspecies. It is prominent but rounded and forms a conspicuous shoulder. The spire has a tendency to be flatter and less immersed than in *Helisoma anceps* (*s. str.*) and the collabral sculpture is remarkably coarse and reminiscent of the sculpturing of *H. trivolvis corpulentum* which occurs in approximately the same region. See " Remarks " under *H. anceps* (*s.str*).

Measurements:

See Text Fig. 9 and " Remarks " under *Helisoma anceps* (*s. str.*) for explanation of abbreviations and measurements; see Charts 27 to 33 (populations 11–15) for additional measurements.

Feature	N	Range	Mean	S.E.$_M$	S.D.
Kenogamisis Lake, 7 mi SE of Geraldton, Ont.					
Max. Dia., mm	30	5·1 —16·9	12·34	—	—
Gr. Dia., mm	30	5·1 —16·9	12·01	—	—
Height (H), mm	30	4·0 —10·4	7·50	—	—
Umbil. Dia., mm	30	2·6 — 9·2	6·18	—	—
Umbil. Dia./Gr. Dia.	30	0·45 — 0·65	0·516	0·008	0·042
Whorls	30	2·9 — 4·5	3·95	—	—

Feature	N	Range	Mean	S.E.$_M$	S.D.
Frog Rapids, Abram Lake, Sioux Lookout, Ont.					
Max. Dia., mm	30	4·6 —13·4	8·95	—	—
Gr. Dia., mm	30	4·6 —12·2	8·50	—	—
Height (H), mm	30	3·0 — 7·3	5·26	—	—
Umbil. Dia., mm	30	2·7 — 6·4	4·61	—	—
Umbil. Dia./Gr.. Dia.	30	0·46 — 0·64	0·545	0·007	0·041
Whorls	30	2·4 — 4·2	3·28	—	—

Records:

Albany River system. Kenogamisis Lake, 7 mi SE of Geraldton, Ont. Hutchinson Lake, 5 mi N of Geraldton. Medcalfe Lake (2 localities), 60 and 63 mi N of Savant Lake, Ont. Pelican Lake, Sioux Lookout, Ont. (all this survey). Lake St. Joseph, Ont. (1904, W. McInnes !; 1929, A. R. Cahn!). Hamilton Lake, Sioux Lookout District, Ont. (Baker & Cahn, 1931: 55). Lake Nipigon (1884, J. Macoun !).

Attawapiskat River system. Kawinogans River, northern Ont. (1904, W. McInnes!).

Winnipeg River system. Cat Lake, Botsford Lakes, and outlet of Bamaji Lake, Sioux Lookout District, Ont. (Baker & Cahn, 1929: 55). Bamaji Lake, Ont. (1929, A. R. Cahn!). Sturgeon River[Marchington River], 1 mi W of Superior Junction, Ont. Frog Rapids, Abram Lake, Sioux Lookout, Ont. Inlet of small lake 8 mi W of Sioux Lookout. Chukuni River, 2 mi E of Red Lake, Ont. (all this survey).

Distribution: *Helisoma anceps royalense* is known with certainty only from Isle Royale, Lake Superior, and the adjacent portion of Ontario north and west of Lake Superior in parts of the Albany, Attawapiskat, and Winnipeg River systems (see Map 81). The holotype of *H. a. rushi* F. C. Baker (1939b, fig. 1, middle row) appears to be identical to many specimens of *H. a. royalense* and if its source population is similar the range of *H. a. royalense* also extends into Georgian Bay. See "Remarks" below.

Biology and Ecology: This subspecies was collected at 9 localities during this survey. Five of these are large lakes, 1 is a small lake, 1 is a short, strongly-flowing river-like connection between 2 lakes (Frog Rapids, Abram Lake) and 2 are large, slow-flowing rivers. Vegetation was of medium abundance at 7 localities and thick at 2. Bottoms were all of mixed types but sand was present in considerable quantity at 8 localities. *Helisoma anceps royalense* occurred frequently on rocks and on logs but was also taken from vegetation by sweeping with a net.

The anatomy of *Helisoma anceps royalense* has not been examined in detail but it does not appear to differ significantly from that of other populations of *H. anceps*. The radula formula, according to Baker (1945: 128) is 25-1-25 to 27-1-27 for Bamaji Lake specimens.

Remarks: The National Museum of Natural Sciences has a specimen of *Helisoma anceps royalense* collected by Dr. J. L. Chamberlin in 1950 from brown soil in the bank of the Moose River at Moosonee, Ontario, about 10 feet above waterline. The population now living in the Moose and Kwataboahegan rivers at their junction, about 12 mi S of Moosonee, appears to be made up of intergrades between *H.a. anceps* and *H. a. royalense* (see Chart 34, population sample 21). Some additional samples from that region also exhibit a tendency toward shouldered

carinae while other samples do not. The evidence, such as it is , implies that *H. a. royalense* may have extended to the Moosonee region in the post-Pleistocene and, although it became swamped by the subsequent invasion of *H. a. anceps*, *H. a. royalense* genes still persist in the present population in that area.

Subgenus *Planorbella* Haldeman

Planorbella Haldeman, 1842: *Monograph of the freshwater univalve Mollusca of the United States*. Physadae, p 14, pl. 1 [under *Planorbis*]. Type, by original designation, *Planorbis campanulatus* Say.

Hypsogyra Lindholm, 1927: Kritische Studien zur Molleskenfauna des Baikalsee. *Travaux de la Commission pour l'Etude Lac Bajkal, 2*: 181 (Leningrad *2*: 139-186) (New name for *Adula* H. Adams, 1861 *non* H. & A. Adams, 1857; *Ancaeus* H. Adams, 1869, *non* L. Agassiz, 1846). Type, by original designation, *Planorbis multivolvis* Case.

Shells medium-sized, sinistral, orthostrophic, with a few closely-coiled whorls and with an aperture which is constricted behind and then expanded and bell-like in front. Apex flat or raised to form a low or (rarely) a moderately high spire. Whorls not carinate.

The anatomies of the species and of " subspecies " of *Planorbella* have been admirably described by Baker (1945: 151). They are the same and do not differ in any important way from *Pierosoma*. *Planorbella* is a North American subgenus, of few species, confined to northern United States and to Canada. Geologic range: Late Pleistocene (Wisconsin) to Recent (La Rocque, 1963: 27, etc.).

Helisoma (*Planorbella*) *campanulatum campanulatum* (Say)

Plate 13, Figs. 9-11; Pl. 26, Figs. 7-9; Map 82.

Planorbis campanulatus Say, 1821: *J. Acad. natr. Sci. Philad., 2*: 166 (Binney reprint, 1858: 64). Type locality: " small streams which discharge into Cayuga Lake [New York]. "

Planorbis (*Planorbella*) *campanulatus* variety *rudentis* Dall, 1905: *Land and fresh water mollusks of Alaska and adjoining regions*. Harriman Alaska Exped., *13*: 90. Type locality: " Knee Lake, Hayes River, Keewatin, N. Lat. 55°."

Planorbis campanulatus wisconsinensis Winslow, 1926: *Occ. Pap. Mus. Zool., Univ. Mich.*, No. 180: 5, pl. 2, figs. 14-16. Type locality: " Little Arbor Vitae Lake, Vilas County, Wisconsin. "

Planorbis companulatus davisi Winslow, 1926: op. cit., p 8, pl. 2, figs. 17-19. Type locality: " Pinnebog River, Huron County, Michigan. "

Helisoma campanulata canadensis Baker & Cahn, 1931: *Nat. Mus. Can. Bull.*, 67: 57, pl. 2. Type locality: " Bamaji Lake, northern Ontario. "

Diagnosis: Shell medium to large, planorboid, sinistral, rounded, apex more or less flattened, and with an expanded, bell-shaped aperture.

Description: Shell medium-sized to large (up to ⅔ inch in diameter), planorbiform, with up to 7 whorls, ultrasinistral, variable, brownish, and with a more or less flattened spire and a bell-shaped aperture. Early whorls on left (apical) side all visible and slightly immersed below penultimate whorl, which may extend perceptibly above the body whorl. (In some populations the apex is elevated into a low, blunt spire, but the mean value of spire projection does not exceed 5% of the height of the body whorl measured in front of the aperture in the populations observed; see " Remarks "). Right (umbilical) side commonly exhibiting only the ultimate and penultimate whorls, and sometimes part of the next earlier whorl. Umbilicus narrow, deep, and extending to the apex of the shell. Collabral sculpture consisting of rather coarse, closely spaced, raised threads. Spiral sculpture obsolete or very fine. Aperture abruptly expanded, inverted ear-shaped, opisthocline (i.e., directed slightly upward), and with a parietal callus. In many specimens coiling is slightly irregular.

TABLE 9. Statistical analysis of *Helisoma campanulatum* (*s. lat.*).

See " Remarks ". Samples marked with an asterisk represent *H. campanulatum collinsi*, discussed on later pages.

Sample No.	Locality	N	Max. Dia., mm	Gr. Dia., mm	Hgt./Gr. Dia.	Whorls
1	Churchill River, north of La Ronge, Sask.	3	11·1-(11·5)-11·9	9·6-(9·9)-10·5	0·454-(0·468)-0·486	4·1-(4·5)-5·0
2	Lac la Ronge, La Ronge, Sask.	5	10·7-(12·7)-15·1	8·6-(10·5)-12·0	0·417-(0·435)-0·467	4·6-(5·0)-5·4
3	Opachuanau Lake, Sask.	34	10·8-(13·0)-15·3	9·1-(10·9)-12·9	0·465-(0·564)-0·614	4·0-(4·7)-5·1
4	Little Churchill River, Man.	4	9·0-(10·6)-11·4	7·8-(8·9)- 9·4	0·447-(0·475)-0·500	4·4-(4·6)-5·0
5	Severn Lake, Ont.	5	9·2-(9·7)-10·6	7·6-(8·5)- 9·8	0·462-(0·482)-0·533	3·9-(4·2)-4·5
6	Hazel Creek near Hazel, Man.	11	9·2-(10·2)-11·8	7·9-(8·5)- 9·8	0·456-(0·503)-0·539	4·3-(4·7)-5·1
7	Pelican Lake, Orr, Minn.	27	10·7-(11·6)-12·4	9·0-(9·7)-11·1	0·466-(0·529)-0·588	4·5-(4·8)-5·5
8	Lake near Finland, Ont.	4	9·8-(10·4)-11·0	8·3-(8·6)- 9·1	0·549-(0·600)-0·626	4·6-(4·7)-4·8
9	Lake of the Woods, Kenora, Ont.	10	10·0-(11·8)-12·7	8·6-(9·6)-10·1	0·387-(0·413)-0·460	4·5-(5·0)-5·3
*10	Wabaskang Lake, north of Vermilion Bay, Ont.	15	10·5-(12·7)-14·4	8·7-(10·2)-11·6	0·403-(0·491)-0·562	5·2-(6·0)-6·5
*11	Red Lake, Cochenour, Ont.	15	8·2-(8·8)- 9·4	7·7-(8·0)- 8·7	0·513-(0·576)-0·636	5·0-(5·3)-5·6
*12	Paguchi Lake near Ignace, Ont.	15	11·5-(12·7)-14·3	9·6-(10·5)-11·4	0·528-(0·597)-0·658	4·9-(5·1)-5·6
15	Klotz Lake near Longlac, Ont.	30	10·8-(12·3)-15·9	8·7-(9·8)-12·6	0·433-(0·470)-0·518	5·0-(5·9)-6·6
16	St. Ann's Lake, Fort Albany, Ont.	8	8·7-(10·1)-12·4	7·5-(8·6)- 9·8	0·484-(0·521)-0·566	4·6-(4·9)-5·3
17	Lake near Kapuskasing, Ont.	25	10·5-(12·4)-14·3	9·1-(10·5)-12·0	0·447-(0·509)-0·588	5·2-(5·9)-6·4
18	Lillabelle Lake near Cochrane, Ont.	16	8·0-(10·5)-12·3	7·4-(9·0)-10·4	0·430-(0·500)-0·541	4·0-(5·1)-5·8
19	Pond near Matheson, Ont.	20	10·2-(11·0)-12·2	8·7-(9·3)-10·2	0·405-(0·434)-0·459	4·0-(4·9)-5·6

Records:

Because of uncertainties regarding subspecific assignments by other workers only specimens examined are included.

Harricanaw River system. Lac Dubuisson, E side, 5 mi NW of Val d'Or, Que. (this survey).

Moose River system. Abitibi River drainage area: Duparquet River, 3 mi N of Rapide Danseur, Que. Pond 6 mi S of Matheson, Ont. Pond 10 mi S of Cochrane, Ont. Lillabelle Lake, 3 mi and 5 mi N of Cochrane (all this survey). Mattagami River drainage area: small lake 10 mi E of Kapuskasing, Ont. (this survey).

Albany River system (all records, Ontario). Forde Creek, 25 mi W of Hearst. Klotz Lake, 30 mi E of Longlac. Lake 20 mi E of Beardmore. Metcalfe Lake, 60 mi N of Savant Lake (all this survey). Hamilton Lake (50° 50′N, 90°29′W) (1929, A. R. Cahn!). Lake St. Joseph (51°N, 91°W) (1904, W. McInnes!). Lake St. Joseph, Rat Rapids. St. Ann's Lake, Sinclair Island, Fort Albany (both this survey).

Attawapiskat River system (all records, Ontario). Attawapiskat Lake (1903, W. McInnes!). Kawinogans River [=Crow River]. "Elbow", Otoskwin River. (both 1904, W. McInnes!).

Winisk River system. Wapikopa Lake, Winisk River, Ont. (1904, W. McInnes!).

Severn River system. Deer Lake, Ont. (52° 38′N, 94°25′W) (1960, Ont. Dept. Lands and Forests!). Severn Lake (54°N, 90°40′W) N and S ends, Ont. MacDowell Lake (52°14′N, 92°47′W), Ont. Sandy Lake, Sandy Lake village, (53°00′N, 93°20′W), Ont. (all this survey).

Hayes River system. Island Lake, Island Lake village, (53°50′N, 94°40′W), Man. Stull Lake, at outlet (54°29N, 92°37′W), Ont. Knee Lake, near outlet and at northern narrows (55°10′N, 94°25′W; 55°04′N, 94°45′W), Man. (all this survey).

Winnipeg River system. Nugget Creek, 12 mi E of Dryden, Ont. Pelican Lake, Sioux Lookout, Ont. Frog Rapids, Abram Lake, Sioux Lookout (all this survey). Bamaji Lake (51°10′N, 91°30′W), Ont. (1929, A. R. Cahn!, "cotypes" of *Helisoma campanulatum canadensis* Baker; also this survey). Cat Lake (51°40′N, 91° 50′W), Ont. (1929, A. R. Cahn!). Sturgeon River [Marchington River], 1 mi W of Superior Junction, Ont. (this survey). Lac Seul, Ont, (1904, W. McInnes! and 1919, F. W. Waugh!). Bug River, 8 mi S of Red Lake, Ont. Chukuni River, 2 mi E of Red Lake. Vermilion Lake, Vermilion Bay, Ont. Chadwick's Lake, 15 mi E of Kenora, Ont. Pelican Lake, Orr, Minn. (all this survey). Sturgeon Lake (48°28′N, 91°40′W), Ont. Basswood River Rapids, Ont.-Minn. International Boundary (both 1931, A.R. Cahn!). McCawlay Creek, 15 mi W of Atikokan, Ont. Lake 12 mi S of Sioux Narrows, Ont. Off Lake, 4 mi NE of Finland, Ont. Outlet of Off Lake. One-Sided Lake [Caliper Lake], 60 mi SE of Kenora, Ont. Lake of the Woods, Kenora, Moth Lake, 25 mi W of Kenora. Winnipeg River, 3 mi E of Fort Alexander, Man. (all this survey.)

Brokenhead River system. Hazel Creek, 2 mi E of Hazel, Man. Brokenhead River, 4 mi E of Vivian, Man. (both this survey).

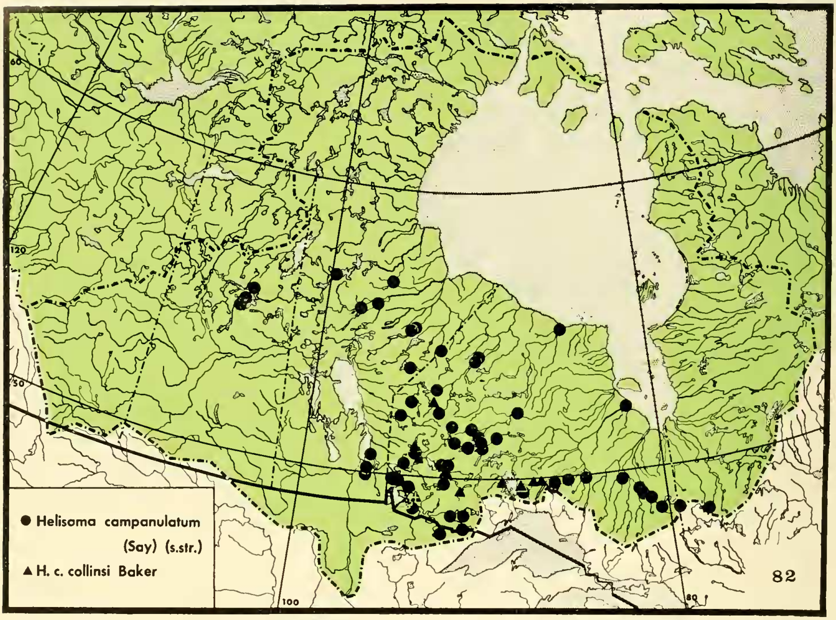
Nelson River system. Cormorant Lake, Man. Burntwood River, Man. (both 1906, W. McInnes!). Stout Lake, at outlet (52°08′N, 94° 44′W), Ont. (this survey).

Churchill River system. Lac la Ronge, La Ronge, Sask. Waden Bay, Lac la Ronge, 17 mi N of La Ronge. Otter Rapids, Churchill River, 54 mi N of La Ronge. Opachuanau Lake (56°44′N, 99° 37′W), Man. (all this survey). Little Churchill River (56° 45′N, 96°W), Man. (1906, O. O'Sullivan!).

Distribution: Newfoundland to southern Quebec and northwest to northern Saskatchewan; Massachusetts to Illinois and North Dakota.

Biology and Ecology: Mozley (1938: 107), under *Planorbis* (*Helisoma*) *campanulatus wisconsinensis*, gives the ecology of this species as follows: " Small lakes, and also to some extent in those of moderate size. Frequently found on bare stones and rock faces, but not in the most exposed situations. This variety is confined to the forested region." Baker (1928a: 347, 350, 352) indicates that in Wisconsin " typical " *Helisoma campanulatum* and *H. c. wisconsinensis* [=*H. c. campanulatum*] are lake species but that the Pleistocene subspecies *H. c. ferrissi* Baker apparently occurred in rivers.

Forty-seven lots of *Helisoma campanulatum campanulatum* were collected during this survey and all were found in the forested region. Of these, 25 are from large lakes, 7 are from small



lakes, 2 are from permanent ponds, and 13 are from rivers, but primarily from slow-flowing or backwater areas in these rivers. The rivers were of various widths from about 20 feet to over a mile. In only 1 case were specimens found in a strong current, at Frog Rapids, Sioux Lookout, Ontario, a wide, deep channel connecting 2 large lakes. Here the snails were found on rocks in shallow water. Vegetation was abundant or moderately abundant in nearly all localities but 2, in which it was sparse, and bottoms were of all types. Associated species included many lymnaeids, planorbids (especially other species of *Helisoma*), etc.

The anatomy of *Helisoma campanulatum* has been discussed at length by Baker (1945: 151-153). The living animal is very slow in movement, reddish brown to blackish in colour, and similar to *H. trivolvis* in all characters examined. The radula formula is stated as varying from 20-1-20 to 23-1-23. One specimen from Severn Lake, Ont. (NMC 28964), with a diameter of 11·6 mm, had a radula with 12 marginal teeth bearing 5 to 6 cusps, 8 lateral teeth bearing 3 cusps, and a bicuspid central (only 1 side of the radula could be counted).

Remarks: Following the procedures adopted in this study, all characters considered significant by previous workers were examined and quantified, and numerous population samples from the whole region occupied within the Canadian Interior Basin were analyzed statistically. Characters examined quantitatively were (1) maximum diameter, (2) greater diameter (measured just behind the apertural expansion), (3) the ratio of maximum height divided

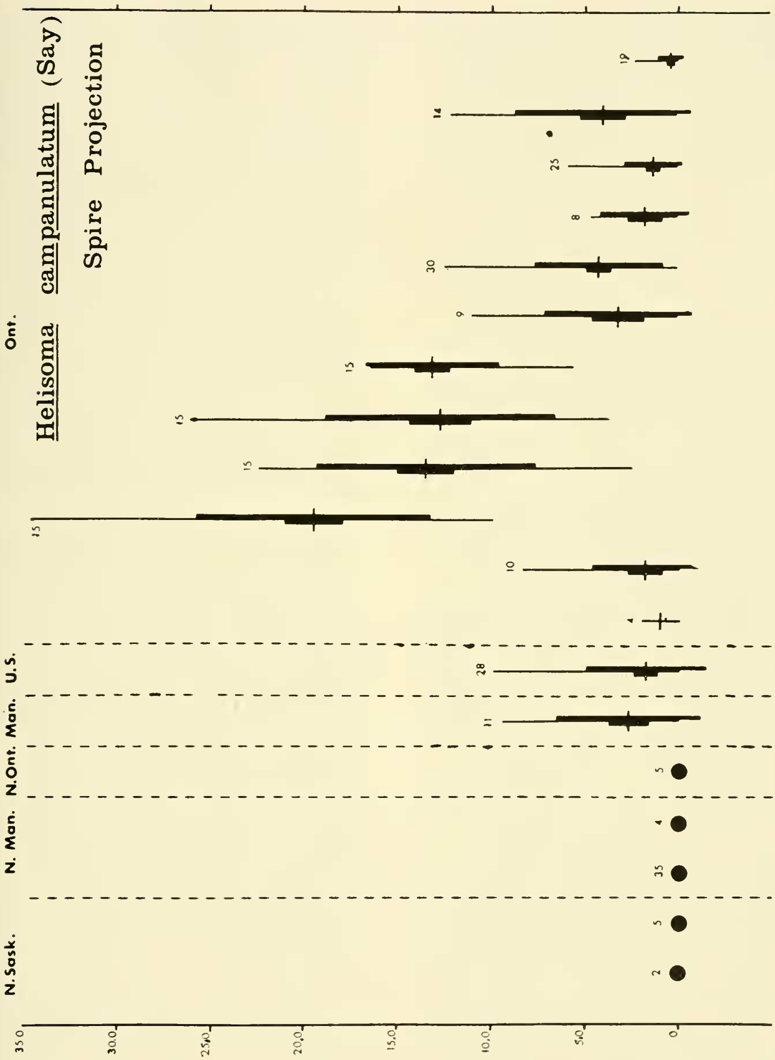


CHART 35. *Helisoma campanulatum* populations. For explanation see p 450.

by greater diameter, (4) whorl count taken from the left or spire side, and (5) spire projection. Spire projection, as used here, is the maximum height of projection of all earlier whorls (the spire) above the body whorl measured immediately in front of the aperture and parallel to the axis of the shell. It is expressed as a percentage relative to the height of the body whorl in front of the aperture.

Other characters were also examined in detail but were not found to be revealing. Apertural dimensions and ratios were investigated but these proved to be related to height and diameter and to vary in a similar manner. Whorl counts from the right (umbilical) side were also attempted but later abandoned because in many specimens all the whorls can be seen by examining the umbilicus under magnification and it is often impossible to decide exactly where the umbilicus begins and where to stop counting whorl volutions. Carination of early whorls, development of collabral sculpture, shape of umbilicus, and degree of irregularity in coiling were also examined but appeared to be of no taxonomic significance in this species.

The results of measurements for characters 1-5 were compared with ecology and geography. The first 4 characters (see " Measurements ") show great variation within and between populations and no ecological or geographical trends are apparent. The fifth character, spire projection, *is* related to geography, however, as indicated on Chart 35.

The chart shows that populations 10, 11, 12, and 13 contain the highest spired individuals and that they have mean values for spire development which are considerably higher than those of other populations. It is also apparent that some spire development occurs in other populations but that it is more conspicuous in populations close to populations 10 to 13 than in populations from far away. When mean spire projection values of more than 10% and less than 5% are used to distinguish high-spired from low-spired populations respectively, and all populations, including small population samples not analyzed statistically but nevertheless referable to high- and low-spired types, are plotted on a distribution map (Map 82), it can be seen that the high-spired populations all occur within the region north of Lake Superior between the Wabaskang Lake-Red Lake area in the west, the North Spirit Lake area in the north, and the Lake Nipigon-Kenogamisis Lake area in the east. Even though low-spired populations are also found within this area, the high-spired populations are here considered to represent a separate subspecies. The name which best applies to this subspecies is *Helisoma campanulatum collinsi* Baker, discussed below.

Helisoma campanulatum " variety *rudentis* ", described by Dall from Knee Lake, Manitoba, appears to be slightly divergent from typical *H. campanulatum* but not sufficiently so as to deserve subspecific rank. The 6 specimens from the type locality collected during the present survey *are* rather large and flat. The largest specimen at hand (15·9 mm maximum diameter) is no larger than the largest specimen seen from Klotz Lake near Lake Superior, however, and the ratios of height to greater diameter and other characters mentioned by Dall are also within the range of variation of the Klotz Lake, and other, populations. The maximum size for Knee Lake specimens (17·5 mm) quoted by Dall is greater than that of any specimen seen from elsewhere and this may be significant, but not enough material is available to indicate differences convincingly. *H. campanulatum* variety

rudentis is here considered a synonym of *H. campanulatum* (*s. str.*)

The other named living " varieties " of *Helisoma campanulatum*, which have been reported from the Canadian Interior Basin (see synonymy) are not geographical subspecies but are simply extreme morphs in normally varying populations or individual variations which occur sporadically throughout the range of the species. In this connection it is significant that in F. C. Baker's final work on the Planorbidae (1945: 153), under *H. campanulatum*, he states: " In this area [northern United States and Canada] it varies considerably and several races have been recognized. These appear to be mostly local races, not geographical, possibly environmental variations. "

Helisoma (*Planorbella*) *campanulatum collinsi* Baker

Plate 26, Figs. 10-12; Map 82.

Helisoma campanulatum collinsi F. C. Baker, 1939: *Can. J. Res., 17*(sec. D) (4): 97, fig. 1. Type locality: " Cameron Lake, northeast of Kakagi Lake ([east of] Lake of the Woods). "

Diagnosis and Description: Similar to *Helisoma campanulatum campanulatum* except with a clearly developed spire. Populations in which the mean value of spire projection divided by body whorl height exceeds 10% are considered as *H. c. collinsi*. See " Remarks " below and under *H. c. campanulatum*.

Measurements:

See population samples 10-13 on Chart 35 and also " Measurements " under *H. c. campanulatum*.

Records:

Albany River system. Kenogamisis Lake, 7 mi SE of Geraldton, Ont. Wild Goose Lake, 39 mi W of Longlac, Ont. Blackwater River, Beardmore, Ont. (all this survey). Lake Nipigon, Ont (1884, J. Macoun!).

Winnipeg River system. Paguchi Lake, 7 mi N of Ignace, Ont. Red Lake, Rahill Beach, Cochenour, Ont., Wabaskang Lake, 40 mi N of Vermilion Bay, Ont. (all this survey). Cameron Lake, Otterskin Lake, and Shingwak Lake, all Lake of the Woods district, Ont. (Baker, 1939b: 97-98).

Severn River system. North Spirit Lake, at outlet (52°31′N, 93°02′W), Ont. (this survey).

Distribution: Northwestern Ontario in the headwaters of the Albany, Winnipeg, and Severn River systems.

Biology and Ecology: This subspecies was collected at 7 stations during the survey. Four of these are large lakes, 2 are medium-sized lakes, and 1 is a slow-flowing river about 75 feet wide. Vegetation varied from thick to sparse. Surprisingly the substrate at each station was only of sand or of sand and gravel. Associated species included several lymnaeids, planorbids, sphaeriids, etc.

Nothing has been published regarding the anatomy of this subspecies. One specimen from Blackwater River near Beardmore, Ont. (NMC 39870), with a diameter of 12·3 mm, had a radula formula as follows: $\frac{14}{5\text{-}6} - \frac{8}{3} - \frac{1}{2} - \frac{8}{3} \quad \frac{13}{5\text{-}6}$ (22-1-21).

Remarks: Baker (1939b: 97, fig. 1) has described, in *Helisoma campanulatum collinsi*, a " subspecies " which appears not to be as extreme in spire development as most specimens in the populations from Wabaskang Lake, Red Lake, Paguchi Lake, and Kenogamisis Lake, Ont. On the other hand, these Ontario populations appear to be less extreme in spire development, in whorl count, and in size than the single known population of *Helisoma* [*campanulatum*] *multivolvis* (Case) from Howe Lake, Michigan, discussed by Walker (1907: 61). (Howe Lake is in the Upper Peninsula of Michigan within 1 mile of Lake Superior.) It is difficult to make

proper comparisons because no measurements are given for spire projection by Baker or Walker, and the variation in morphological characters within *H. c. collinsi* and *H. multivolvis* has not been discussed by either author. But it appears that the present populations are morphologically intermediate between *H. c. collinsi* and *H. multivolvis* but a little closer to the former. In order to avoid description of a new subspecies in this already overburdened group, the present populations are assigned to *H. c. collinsi.*

In this species group as in other groups of freshwater molluscs (e.g., see *Helisoma anceps* and *Valvata sincera*), application of accepted taxonomic procedure is inadequate to characterize all populations. The evidence now available indicates that the high-spired condition is probably controlled by multiple genes; that a large number of these genes probably occur in most individuals of "typical" *Helisoma* [*campanulatum*] *multivolvis*; and that these genes are confined to, but irregularly distributed in, the Lake Superior region and rapidly decrease in frequency beyond this region. Some populations within this region exhibit the high-spired condition to an extent approaching that of *H. c. multivolvis*, other populations exhibit significant but reduced spire development, whereas others have very little or no spire development. Such irregularity may be related to haphazard introductions of individuals by aquatic birds and to the facultative autogamous nature of the species. The high-spired condition is considered to be worth taxonomic recognition because it is distinctive and it is related to geography even though the region occupied is not exclusively populated by the high-spired morph. To use an infrasubspecific name is even more inappropriate because this does not distinguish geographic variants from sporadic non-geographic variants.

Subgenus *Pierosoma* Dall

Pierosoma Dall, 1905: *Land and fresh water mollusks of Alaska and adjoining regions.* Harriman Alaska Exped., *13*: 85. Type species, by original designation, *Planorbis trivolvis* Say.

Shells medium-sized to large, sinistral, orthostrophic, relatively high, of few whorls, and with an aperture which is slightly thickened and, in some species, expanded. Spire depressed or at the same level as the top of the body whorl. Whorls carinate above in most species and carinate below in some. The sinistral character of the shells is particularly obvious in juveniles.

The anatomy of many species and subspecies of *Pierosoma* has been described by Baker (1945: 135-149). See also Hubendick (1955: 534). *Pierosoma* is distinguished from *Helisoma* by peculiarities of the genitalia and radula and by the possession of a longer duct in the penial complex of adult *Pierosoma*. Probably about 25 valid species and subspecies exist. Recent species of *Pierosoma* are confined to North and South America and the West Indies but in the Pleistocene the subgenus also occurred in northeastern Siberia. Geologic range: Pliocene to Recent (Zilch, 1959: 121).

Helisoma (*Pierosoma*) *trivolvis trivolvis* (Say)

Plate 14, Figs. 4-9; Pl.27, Figs. 1-3; Map 83

Planorbis trivolvis Say, 1816: *Nicholson's Encyclopedia.* 1st Amer. ed. *2*, pl. 2: 2 (Binney reprint, 1858: 44). Type locality not specified but Delaware River implied by remarks on following page under *Planorbis parvus*. Specimens larger than that described are cited from "French Creek near Lake Erie", a tributary of the Allegheny River.

Planorbis trivolvis var. *fallax* Haldeman, 1844: *A monograph of the freshwater univalve Mollusca,*

pt. 2, p 15, pl. 3: 1-3. Type locality: " Massachusetts, Lake Erie, Indiana ? "

Planorbis macrostomus Whiteaves, 1863: *Can. Naturalist and Geologist*, *8*: 113, fig. 12. Type locality (op. cit. p 104): " Ponds near Mile-end toll-gate, Montreal. "

Diagnosis: Shell medium to large, planorboid, sinistral, whorls subcarinate to rounded above and rounded below, and with axial height of most adult specimens exceeding 12 mm.

Description: Shell medium to large (up to 1¼ inch in diameter and 3/5 inch in axial height), planorbiform, with up to 5 whorls, sinistral, yellowish-brown to brown, whorls rounded below and subcarinate or rounded above, body whorl laterally convex. Apical depression wide, of moderate depth, and with all preceding whorls clearly visible. (Early whorls rounded or subcarinate and apical depression therefore without the smooth sides characteristic of *Helisoma pilsbryi infracarinatum*). Umbilical region sunken and exhibiting 3 to 3½ whorls. Aperture expanded, ovate ear-shaped, wider than high or approximately equally wide and high, and with a reddish-brown or purplish band within the aperture of most specimens. Sculpture moderate and consisting of collabral riblets, approximately 2 to 4 per mm, and irregularly-spaced growth ridges.

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Montreal Lake, 1 mi N of Montreal Lake, Sask.					
Max. Dia., mm	30	19·5 —28·7	24·8	—	—
Gr. Dia., mm	30	18·8 —28·2	23·7	—	—
Gr. Height, mm	30	10·4 —15·6	12·2	—	—
Gr. Hgt./Gr. Dia.	30	0·463— 0·622	0·521	0·007	0·036
Riblets/5 mm *	29	11—19	14·6	0·4	2·3
Lake 71 mi N of Savant Lake, Ont.					
Max. Dia., mm	32	20·5 —28·0	23·7	—	—
Gr. Dia., mm	32	18·6 —26·6	22·3	—	—
Gr. Height, mm	32	10·2 —12·9	11·4	—	—
Gr. Hgt./Gr. Dia.	32	0·447— 0·570	0·511	0·005	0·028
Riblets/5 mm *	30	13—24	18·5	0·5	2·9
Klotz Lake, 30 mi E of Longlac, Ont.					
Max. Dia., mm	11	22·3 —31·7	28·7	—	—
Gr. Dia., mm	11	21·3 —30·9	27·7	—	—
Gr. Height, mm	11	11·0 —13·9	12·7	—	—
Gr. Hgt./Gr. Dia.	11	0·417— 0·525	0·458	0·011	0·036
Riblets/5 mm *	7	9—15	12·0	0·8	2·0

Feature	N	Range	Mean	S.E.$_M$	S.D.
Lillabelle Lake, 5 mi N of Cochrane, Ont.					
Max. Dia., mm	35	21·9 —28·4	24·8	—	—
Gr. Dia., mm	35	19·0 —27·4	23·3	—	—
Gr. Height, mm	35	10·2 —14·8	12·6	—	—
Gr. Hgt./Gr. Dia.	35	0·448— 0·654	0·541	0·007	0·045
Riblets/5 mm *	33	10—22	14·6	0·5	2·7

* Measured immediately in front of the aperture.

Records:

Eastern Hudson Bay and eastern James Bay drainage areas. Bloody Island Camp, Belcher Islands, N.W.T. (1958, Fish, Res. Bd.!).

Chibougamau River system. Caché Lake, 4 mi S of Chibougamau, Que. Lac Gabrielle, 10 mi S of Chibougamau. SW end of Lac Doré, 10 mi SE of Chibougamau (all this survey).

Harricanaw River system. Hannah Bay, 2 mi above mouth of Harricanaw River, southern James Bay (1904, J. Spreadborough!; reported as *H. plexatum* by Baker (1936: 14, pl. 3: 11-12)). These specimens and those from Belcher Islands cited above appear to be *H. trivolvis* stunted from living in slightly brackish water.

Moose River system. Inlet of Frederickhouse Lake, 6 mi W of Porquis Junction, Ont. Lillabelle Lake, 3 mi and 5 N of Cochrane, Ont. Abitibi River, 17 mi N of Cochrane. Inlet of Remi Lake, at Remi Lake, 14 mi E of Kapuskasing, Ont. Small lake 11 mi ESE of Kapuskasing (all this survey).

Albany River system. Klotz Lake, 30 mi E of Longlac, Ont. Small stream entering W end of Klotz Lake. Lydia Lake, 23 mi E of Longlac. North end of Long Lake, Longlac. Small lake 3 mi N of Geraldton, Ont. Wild Goose Lake, 12 mi E of Jellicoe, Ont. (all this survey). Lake Nipigon (1884, J. Macoun!). Pashkokogan Lake, Ont. (1929, A. R. Cahn!). Lake 71 mi N of Savant Lake, Ont. Yellow Creek and small headwater lake near Fort Albany, Ont. (all this survey).

Attawapiskat River system. Machawaian Lake and Ozhiski Lake, Ont. (both 1904, W. McInnes!). Inlet of Monument Channel at portage from Attawapiskat River, 20 mi W of Attawapiskat, Ont. (this survey).

Winisk River system. West end of Shibogama Lake, Ont. (53°31′N, 88°35′W) (this survey). Wapikopa Lake, Ont. (53°00′N, 87°57′W) (1904, W. McInnes!). Winisk River, Ont. (1903, W. McInnes!).

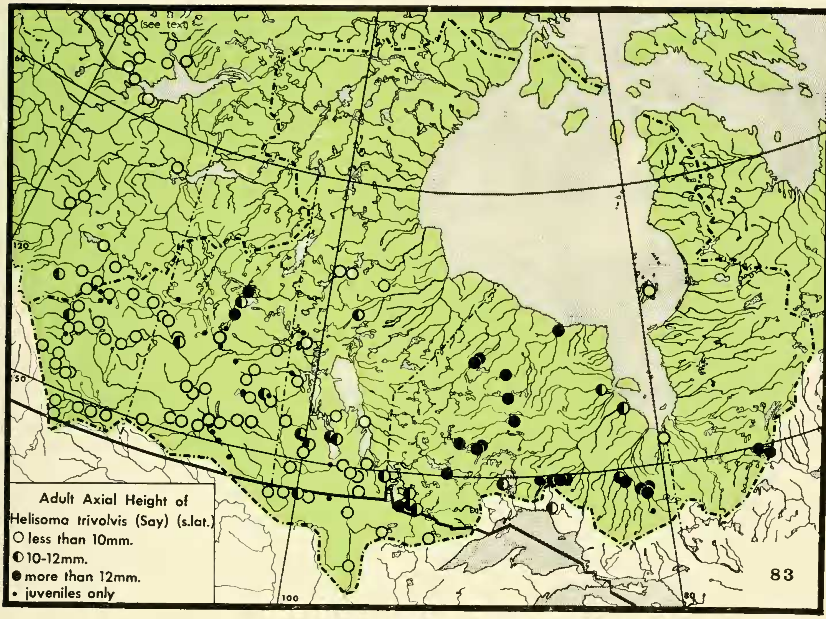
Severn River system. Severn Lake, south end (54°00′N, 90°40′W) and north end (54°05′N, 90°42′W), northwestern Ont. (both this survey).

Winnipeg River system. Rainy River—Lake of the Woods drainage area: Sand Lake, 8 mi N of Virginia, Minn. (this survey). Rainy River, Ont. (1960, Sheila M. Clark!). Lake 12 mi S of Sioux Narrows, Ont. Rainy Lake, 2 mi E of Fort Frances, Ont. Small stream 3½ mi E of Finland, Ont. Little Pine Lake, Finland (all this survey). English River drainage area: Outlet of Bamaji Lake, Ont. (1929, A. R. Cahn!). Bamaji Lake in cove at island (51° 10′N 91°25′W), Ont. Pelican Lake, Sioux Lookout, Ont. (both this survey). Winnipeg River drainage area: Lake in Ewart Township, Ont., 2 mi E of Man.-Ont. boundary (1964, F.R. Cook and J. C. Cook!). Falcon Lake, east end, 2 mi W of Man.-Ont. boundary (this survey).

Saskatchewan River system. Mystic Creek, 30 mi S of Flin Flon, Man. Rocky Lake, 29 mi N of The Pas, Man. (both this survey). Cormorant Lake, Man. (54°14′N, 100°49′W) (1906, W. McInnes!).

Nelson River system. Wintering Lake, Thicket Portage, Man. (1936, R. W. Smith!).

Churchill River system. Bittern Creek, 15 mi N of Waskesiu Lake, Sask. Montreal River, 1 mi N of Montreal Lake, Molanosa, Sask. Potato Lake, 7 mi S of La Ronge, Sask. Lac la Ronge, La Ronge. Midway Lake, 13 mi NNW of La Ronge. Nemeiban River, "Old Fishing Point", 20 mi N of La Ronge. Lynx Lake, 29 mi N of La Ronge. Reindeer Lake, Brochet, Man. Opachuanau Lake, Man. (56°44′N, 99°37′W) (all this survey).



Distribution: Throughout the boreal forest region in the Canadian Interior Basin (as indicated above) east to the Maritime Provinces and New England and south in the United States. It is not reported from Newfoundland (Brooks & Brooks, 1940). Other subspecies occur in the southern United States and the locations of the areas of contact between these and *Helisoma trivolvis trivolvis* have not been determined.

Biology and Ecology: Among the 41 collections of *Helisoma trivolvis trivolvis* from the present survey, 30 occurred in lakes of various sizes, 1 in a permanent pond, and 10 in streams of diverse widths of over 100 feet to approximately 10 feet. In the stream localities current was moderate in 1, slow in 7, and not perceptible in 2. Vegetation was present at all stations and was moderate to thick at most localities. Bottom sediments were of all types but mud was most frequent and was dominant at 32 localities. *H. t. trivolvis* occurred among submersed vegetation or on rocks in the habitats sampled. These observations show that *H. t. trivolvis* is characteristic of eutrophic, permanent-water habitats and that it occurs most frequently as an element of complex molluscan communities containing many species. *Lymnaea stagnalis* and other planorbids, etc. are often found in association with *H. t. trivolvis*.

The anatomy of this species has been discussed in detail by Baker (1945: 135-150). The radula formula is given (loc. cit.) as 23-1-23 to 26-1-26 for specimens of "*trivolvis*" from New York and Wisconsin and 27-1-27 to 39-1-39 for specimens of "*macrosto-*

mum " from Wisconsin, Saskatchewan, and Quebec. Specimens from the research area examined for radulae gave results as follows:

Locality	Cat. No.	Max. Dia., mm.	Radula Formula
Montreal River, Sask.	19559 A	23·0	$\frac{19}{4\text{–}5}-\frac{13}{3\text{–}4}-\frac{1}{2}-\frac{13}{3\text{–}4}-\frac{18}{4\text{–}5}$ (32–1–31)
Severn Lake, Ont.	23955 A	25·6	$\frac{21}{4\text{–}5}-\frac{13}{3}-\frac{1}{2}-\frac{13}{3}-\frac{20}{4\text{–}5}$ (34–1–33)
Severn Lake, Ont.	23955 B	25·1	$\frac{19}{4\text{–}5}-\frac{13}{3}-\frac{1}{2}-\frac{13}{3}-\frac{18}{4\text{–}5}$ (32–1–31)

Remarks: More than 100 lots of *Helisoma trivolvis* (*s. lat.*) were collected during the survey and an equal number of additional lots are in the National Museum of Natural Sciences from the region under investigation. When these are compared with each other and with extralimital collections, much confusing variation is seen. Two general trends are apparent, however: (1) a gradual, irregular increase in size as one moves from the eastern United States northward into eastern Canada and the Hudson Bay drainage area and (2) a relatively abrupt decrease in axial height as one moves from eastern Canada into the prairies of western Canada. The former shift leads to the large morph named *Planorbis macrostomus* by Whiteaves and recognized as a subspecies of *H. trivolvis* by Baker. The shift is so incomplete, irregular, and gradual, however, that it is incorrect to retain the large northern morph as a distinct subspecies.

The decrease in axial height observed when crossing from the boreal forest into the prairies is much more sudden, (see Map 83). Other characters, e.g., apical carination and frequency and prominence of riblets are variable and do not show the same geographical relationships. " Looseness " of coiling is more apparent in prairie populations but is related to the same factors which result in decreased axial height, i.e., smaller diameter of the helicone. Intermediate populations occur in the zone of contact, however, and since the division is based on essentially a single character, subspecific status for the prairie populations is considered proper. That subspecies, *Helisoma trivolvis subcrenatum* (Carpenter), is discussed below.

Helisoma (*Pierosoma*) *trivolvis subcrenatum* (Carpenter)
Plate 26, Figs. 13-15; Map 83.

Planorbis subcrenatus Carpenter, 1856: *Proc. zool. Soc. London*, p 220-221. Type locality: " Oregon. "

Planorbis hornii Tryon, 1865: *Amer. J. Conchol.*, *1*: 231, pl. 22: 16. Type locality: " Fort Simpson, British America " [probably British Columbia, see Baker, 1936: 14].

Planorbis plexatum Ingersoll, 1876: *Report on the natural history of the United States geological and geographical survey of the territories.* Ann. Rept. U. S. Geol. & Geog. Surv. Territ. 1874, p 402. Type locality: " St. Mary lake, Mineral county, Colorado. "

Diagnosis and Description: Similar to *Helisoma trivolvis trivolvis* except that

H. t. subcrenatum exhibits shorter axial height, more loosely coiled whorls, and deeper sutures. The axial height (=greater height) of adult *H. t. subcrenatum* is less than 10 mm in most populations, whereas the axial height of adult *H. t. trivolvis* is more than 12 mm in most populations and exceeds 10 mm in virtually all populations. The diameter of the helicone is uniformly less in *H. t. subcrenatum* than in *H. t. trivolvis*. Some specimens of *H. t. subcrenatum* also exhibit spiral, pale-coloured streaks or irregular coiling but these characters occur in only a few populations. The 2 subspecies also occupy distinct ecological and geographical areas (see Map 83).

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Second Vermilion Lake, Banff, Alta.					
Max. Dia., mm	20	16·8 —24·8	20·9	—	—
Gr. Dia., mm	20	16·2 —23·3	19·2	—	—
Gr. Height, mm	20	6·8 —10·3	8·5	—	—
Gr. Hgt./Gr. Dia.	20	0·376— 0·498	0·443	0·004	0·024
Riblets/5 mm *	15	11—20	15·7	0·6	2·2
Chin Lake, 13 mi E of Lethbridge, Alta.					
Max. Dia., mm	10	14·3 —20·7	17·8	—	—
Gr. Dia., mm	10	13·5 —19·4	16·9	—	—
Gr. Height, mm	10	6·8 — 9·5	8·3	—	—
Gr. Hgt./Gr. Dia.	10	0·461— 0·517	0·491	0·005	0·017
Riblets/5 mm *	10	15—23	18·9	0·7	2·1
Loch Leven, Cypress Hills Provincial Park, Sask.					
Max. Dia., mm	23	13·5 —21·1	17·8	—	—
Gr. Dia., mm	23	13·2 —20·4	16·8	—	—
Gr. Height, mm	23	6·1 — 9·1	7·8	—	—
Gr. Hgt./Gr. Dia.	23	0·369— 0·498	0·464	0·006	0·031
Riblets/5 mm *	20	14—23	18·0	0·6	2·6
Township 44, Range 26, West of First Meridian, Man.					
Max. Dia., mm	25	17·1 —23·4	20·7	—	—
Gr. Dia., mm	25	16·1 —22·2	19·5	—	—
Gr. Height, mm	25	6·7 — 9·7	8·5	—	—
Gr. Hgt./Gr. Dia.	25	0·375— 0·480	0·421	0·005	0·027
Riblets/5 mm *	25	13—20	16·4	0·4	1·9

* Measured immediately in front of the aperture.

Records:

Since 132 lots are available from the research area only marginal localities are listed.

Brokenhead River System. Hazel Creek, 2 mi E of Hazel, Man (this survey).

Red and Saskatchewan River systems, Lake Manitoba-Lake Winnipegosis drainage area and the following inland drainage systems: Devil's Lake, (N.D.) Quill Lakes and Reeds Lake (Sask.) and Chin Coulée (Alta.). Abundant throughout.

Nelson River system. Lake St. Martin, west shore, 3 mi SE of Gypsumville, Man. (1964, M. Ouellet!). Black Bear Island, Lake Winnipeg, Man. (1890, Dowling and Lamb!).

Churchill River system. 2 mi NE of Bonnyville, Alta. Goodsoil, Sask. 4 mi N of Erinferry, Sask. 10 mi S of Meadow Lake, Sask. 3 mi NW of Meadow Lake (all 1962, F. R. Cook and C. B. Powell!). Bay west of Poplar Narrows, Southern Indian Lake (56°42′N, 98°52′W) (1965, J. V. Wright!). Waskaiowaka Lake, Man. (56°30′N, 96°20′W) (1906, O. O' Sullivan!).

Mackenzie River system. Abundant in the Peace, Athabasca, and Slave River drainage areas and in the vicinity of Great Slave Lake. Marginal records are as follows: Mile 550, Alaska Highway, B.C. (near junction of Coal River and Liard River) (1962, S. D. MacDonald!). Crooked Lake, B.C. (59°52′N, 126°24′W) North Toobally Lake, Y.T. (60°20′N, 126°15′W) (both 1961, P. M. Youngman!). Lac à Jacques, N.W.T. (66°10′N, 127°25′W). Fossil Lake, 8 mi N of Fort Good Hope, N.W.T. (both 1962, Fish. Res. Bd.!). Lakes 30 mi S of Aklavik, N.W.T. (1940, K. H. Lang!).

Distribution: California to British Columbia and Yukon Territory and east to Utah, Colorado, Minnesota, and Manitoba. In Canada east of the Rocky Mountains it is a prairie subspecies. Its southern limits are poorly known.

Biology and Ecology: Sixty-eight lots of *Helisoma trivolvis subcrenatum* were collected during this survey. Of these, 13 lots are from large lakes, 6 are from small lakes, 5 are from permanent ponds, 2 are from backwater areas of rivers and creeks, 5 are from rivers over 100 feet wide, 6 are from rivers 50 to 100 feet wide, 14 are from streams 25 to 50 feet wide, 12 are from streams 10 to 25 feet wide, 1 is from a stream less than 10 feet wide, and 4 are from swamps.

Aquatic vegetation was present at all localities and was abundant at many. Bottom sediments were diverse but muddy substrates were dominant and were recorded from 48 of the 68 sites sampled. Current was recorded as slow at the majority of lotic habitats sampled, but in a few habitats it was rapid, moderate, or imperceptible.

Microecological requirements of *Helisoma trivolvis subcrenatum* were similar to those seen in *H. t. trivolvis*. Associated species were many, with *Lymnaea caperata*, *Gyraulus parvus*, *G. deflectus*, and *Promenetus exacuous megas* frequent.

The anatomy of *Helisoma t. subcrenatum* has been described by Baker (1945: 140-141, pls. 26, 30) under *H. horni*, *H. plexatum*, and *H. subcrenatum*. The radula formulae quoted range from 25-1-25 to 32-1-32. Specimens collected during the present survey had formulae as follows:

Locality	Cat. No.	Max. Dia., mm	Radula Formula
Second Vermilion Lake, Banff Alta.	28186 B	20·1	$\frac{16}{4\text{–}5} - \frac{13}{3\text{–}4} - \frac{1}{2} - \frac{13}{3} - \frac{16}{4\text{–}5}$ (29–1–29)
Second Vermilion Lake, Banff Alta.	28186 C	21·6	$\frac{17}{4} - \frac{13}{3} - \frac{1}{2} - \frac{13}{3} - \frac{17}{4}$ (30–1–30)
Creek near Carstairs, Alta.	29107 A	19·5	$\frac{17}{4} - \frac{12}{3} - \frac{1}{2} - \frac{12}{3} - \frac{16}{4}$ (29–1–28)

Remarks: The specimens recorded were all examined carefully in an attempt to divide them into groups corresponding to *Helisoma horni*, *H. plexatum*, and *H. subcrenatum* as defined by Baker (1936). These taxa are supposedly distinct and largely sympatric. All the characters used by Baker (prominence of riblets and frequency, angulation versus roundness of early whorls, depth of suture, etc.) were found to be variable within populations, however, and no divisions could be made. In later years, Baker (1945, pl. 90, 92, etc.) reduced *H. horni* and *H. plexatum* to subspecific rank under *H. subcrenatum*.

All the characters that supposedly distinguish *Helisoma horni* and *H. plexatum* from *H. t. subcrenatum* are variations occurring sporadically within the range of the latter, at least within the present research area. For this reason the 3 names are considered synonymous.

Furthermore, as pointed out under *Helisoma trivolvis trivolvis*, the plains populations differ from typical *H. trivolvis* in only 1 major character, the maximum diameter of the helicone, and intermediate populations occur in the zone of contact between the 2 taxa. For these reasons the subspecific name *H. t. subcrenatum* (Carpenter) is considered appropriate for these western populations.

Helisoma (*Pierosoma*) *pilsbryi infracarinatum* Baker
Plate 14, Figs. 10-12; Map 84.

Helisoma infracarinatum Baker, 1932: *Nautilus*, *46*(1): 8; Baker, 1936: *Nat. Mus. Can. Bull.* 79: 21-23, pl. 2: 6-15, pl. 4: 15, 16, 20. Type locality: " Basswood River rapids, Rainy River District, western Ontario, Canada. "

Helisoma pilsbryi infracarinatum, Baker, 1945: *The Molluscan Family Planorbidae*, p 138, pl. 25: 8-13, pl. 56: 4-5.

Helisoma kennicotti Baker, 1945: loc. cit., p 223, pl. 89: 13-17. Type locality: " Lake Isle la Crosse, English River, Canada. " Actually Lac Ile-à-la-Crosse, northern Saskatchewan, see " Remarks. "

Helisoma pilsbryi preblei Baker, 1945: loc. cit., p 224, pl. 91: 6-8. Type locality: " Knee Lake, [Hayes River system], Manitoba, Canada. "

Diagnosis: Shell medium to large, planorboid, sinistral, proportionately high, centrally carinate above and centrally carinate or subcarinate below, and with the outer side of the body whorl rounded.

Description: Shell medium to large (up to 1 inch in diameter), planorbiform, with up to $4\frac{1}{2}$ whorls, sinistral, brownish or yellowish, centrally carinate above and below, at least on early whorls. Later whorls on many specimens overlapping or tightly appressed to the central upper carina on the next preceding whorl allowing only the adaxially flattened upper parts of earlier whorls to be exposed. In such specimens the left side appears almost smoothly concave and the suture is visible only as an inscribed line. On other specimens early carinae are not obscured but the adaxially flattened upper parts of early whorls are still clearly apparent. Apical carina sharp, persisting on the body whorl, and located centrally or slightly adaxially. Basal carina apparent on early whorls, present or absent on body whorl, and if present, located centrally or slightly abaxially on the body whorl. Body whorl rounded on outer side. Umbilical region sunken and exhibiting 2 to 3 whorls. Aperture ovate ear-shaped, higher than wide, and with the outer lip reflexed in many specimens. Sculpture moderate and consisting of fine collabral riblets, approximately 2 to 4 per mm.

See " Remarks " for morphological comparisons with related species.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Basswood River Rapids, Ont.—Minn. Boundary (type lot).*					
Max. Dia., mm	2	20·0 —23·0	21·5	—	—
Gr. Dia., mm	6	18·0 —25·5	22·0	—	—
Gr. Hgt., mm	6	10·0 —14·0	11·8	—	—
Gr. Hgt./Gr. Dia.	6	0·512— 0·556	0·540	0·007	0·017
Riblets/5 mm †	2	12 —17	14·5	—	—
Qu'Appelle River, 4½ mi NW of Katepwa, Sask.					
Max. Dia., mm	12	14·6 —17·1	16·1	—	—
Gr. Dia., mm	12	13·5 —16·4	15·3	—	—
Gr. Hgt., mm	12	6·8 —9·1	7·9	—	—
Gr. Hgt./Gr. Dia.	12	0·463— 0·565	0·516	0·010	0·035
Riblets/5 mm	12	15 —29	20·0	0·9	3·2
Montreal Lake, 16 mi N of Waskesiu Lake, Sask.					
Max. Dia., mm	19	16·3 —28·5	22·0	—	—
Gr·Dia., mm	19	15·2 —27·9	20·6	—	—
Gr. Hgt., mm	19	8·2 —14·7	11·7	—	—
Gr. Hgt./Gr. Dia.	19	0·506— 0·706	0·568	0·011	0·047
Riblets/5 mm	15	11 —21	15·2	0·7	2·7

* These values are derived from measurements of 4 specimens (holotype and 3 paratypes) quoted by Baker (1932: 8) and from 2 additional paratypes (No. 3222) in the National Museum of Natural Sciences.

† Riblets are counted on the body whorl immediately in front of the aperture.

Records:

Moose River system. Wilson Lake, 1.5 mi S of Nellie Lake, Ont. (this survey).

Albany River system. Kenogamisis Lake, 7 mi SE of Geraldton, Ont. Small lake 8 mi W of Nakina, Ont. (both this survey).

Attawapiskat River system. Crow River, Central Patricia, Ont. (this survey).

Severn River system. Deer Lake, Ont. (52°38′N, 94°25′W) (1960, Ont. Dept. Lands and Forests!). North Spirit Lake, Ont. (52°31′N, 93°02′W). Unnamed lake at headwaters of Sachigo River, Ont. (53°37′N, 92°40′W) (both this survey).

Hayes River system. Knee Lake, Man. (type locality of *H. pilsbryi preblei* Baker) (Baker, 1945: 224 and this survey). Stull Lake, Ont., at outlet (54°29′N, 92°37′W). Red Sucke Lake, Man., west end (54°10′N, 93°57′W) (both this survey).

Winnipeg River system. Rainy River-Lake of the Woods drainage area: Lac des Mille Lacs swamp, Ont. Basswood River Rapids, Ont-. Minn. boundary (paratypes of *H. infracarinatum*) (both 1931, A. R. Cahn!). English River drainage area: Marchington River [Sturgeon River] Bamaji Lake, Blackstone Lake, and Trout Lake, Ont. (all F. C. Baker, 1936: 22). Inlet of small lake 8 mi W of Sioux Lookout, Ont. (this survey).

Red River system. Red River drainage area: Lake Traverse, Brown's Valley, Minn. (this survey). Assinboine River drainage area: Echo Lake at inlet, Echo Valley Provincial

Park, Sask. (this survey). Echo Lake, Qu'Appelle Valley (1964, D. L. Delorme!). Qu'Appelle Lake, 4½ mi NW of Katepwa, Sask. Qu'Appelle Lake, Katepwa Provincial Park. Qu'Appelle River, 4 mi S of Katepwa. Qu'Appelle River, 11 mi N of Whitewood, Sask. Cut Bank River, 7 mi E of Mohall, N.D. (all this survey).

Lake Manitoba-Lake Winnipegosis drainage areas. Willow Bend Creek, 9 mi W of Portage la Prairie, Man. Lake Winnipegosis, 13 mi N of mouth of Red Deer River, Man. (both this survey). Denbeigh Point, Lake Winnipegosis, Man. (2 localities, both 1964, M. Ouellet!).

Saskatchewan River system. Lake 6 mi SE of Flin Flon, Man. (this survey).

Nelson River system. Sturgeon-weir River, Sask. (54°20'N, 102°W) (1908, W. McInnes!). Wintering Lake, Thicket Portage, Man. (1936, R. W. Smith!). Wekusko Lake, Man. (54°45'N 99°50'W) (1906, W. McInnes!).

Churchill River system. Lac Ile-à-la-Crosse, Sask. (type locality of *H. kennicotti* Baker) (Baker, 1945: 223). Waskesiu Lake. Waskesiu Lake at Heart Lakes Portage, Kingsman Lake, and Crean Lake, all Prince Albert district, Sask. (all Baker, 1937: 116). Montreal Lake, S end, 16 mi N of Waskesiu Lake. Waden Bay, Lac la Ronge, 17 mi N of La Ronge, Sask. White Stone Lake, Man. (56°27'N, 97°30'W). Eden Lake, at outlet, Man. (56°38'N, 100° 15'W) (all this survey).

Mackenzie River system. Lac La Biche, Alta. (*ca.* 1945, J. G. Oughton!).

Distribution: St. Lawrence River drainage area in Georgian Bay and the St. Lawrence River and Rideau River. Canadian Interior Basin from eastern Ontario to central Saskatchewan in the boreal forest region and with isolated populations south of the boreal forest.

Biology and Ecology: Of the 24 lots of *Helisoma pilsbryi infracarinatum* collected during this survey, 16 are from large lakes, 2 are from small lakes, 2 are from rivers over 100 feet wide, 2 are from rivers of 50 to 100 feet in width, and 2 are from creeks only 25 feet wide. Submersed vegetation was present at all localities and of moderate density at most. Bottom sediments were of all types. In lotic environments the current was slow or not evident in the microhabitats occupied by *H. p. infracarinatum*. Several gastropod species occurred along with *H. p. infracarinatum* but the species most frequently found associated is *Lymnaea stagnalis appressa*.

The genitalia and the radula of this subspecies have been described by Baker (1945: 138). The radula formula of mature specimens is given as 30-1-30 to 37-1-37.

Remarks on Distinguishing Characters and Variation: Since reliable criteria are lacking for any new evaluation of the biological relationship between this taxon and the more southern *Helisoma pilsbryi* Baker, the most recent opinion (Baker, 1945: 138) is followed and the name *H. p. infracarinatum* Baker is used.

Baker (1936: 21) has described in some detail the comparative morphological features of this and related species as follows: " Shell [of *H. p. infracarinatum*] resembling *Helisoma pilsbryi* in general form but distinguished by a more or less heavy carina on the centre of the basal whorls; the umbilical region is more sunken and usually exhibits three full whorls, whereas in *pilsbryi* the whorls shown are a trifle less than three; the spire whorls are carinated, the body whorl sharply carinated, whereas they are rounded or bluntly angled in *pilsbryi*; the aperture is greatly expanded below and forms a strongly angled V-shape above with the dorsal carina extending to the aperture, and the lip is heavily reflexed, features absent in *pilsbryi*; *infracarinatum* also has a thicker shell; the sculpture is rib-striate, coarser than in *pilsbryi*; radula formula 32-1-32 to 37-1-37, whereas in *pilsbryi* it is 27-1-27 to 29-1-29. "

" From *corpulentum* it differs in having the carina in the centre instead of

at the edge of the whorl and the sculpture is much finer; from the race *multicostatum* [here synonymized with *H. corpulentum*] it differs in having a rounded instead of a flattened base, a rounded instead of a flattened body whorl, and generally more rounded whorls above and below. *Infracarinatum* is liable to be confused with large forms of *trivolvis* which have a decided carina on the whorls of the upper surface. In the absence of the radula these shells [*H. trivolvis*] may be distinguished by being of much shorter axial height, and by having an aperture wider than high, whereas it is the reverse in the present species." (Baker, 1936: 21).

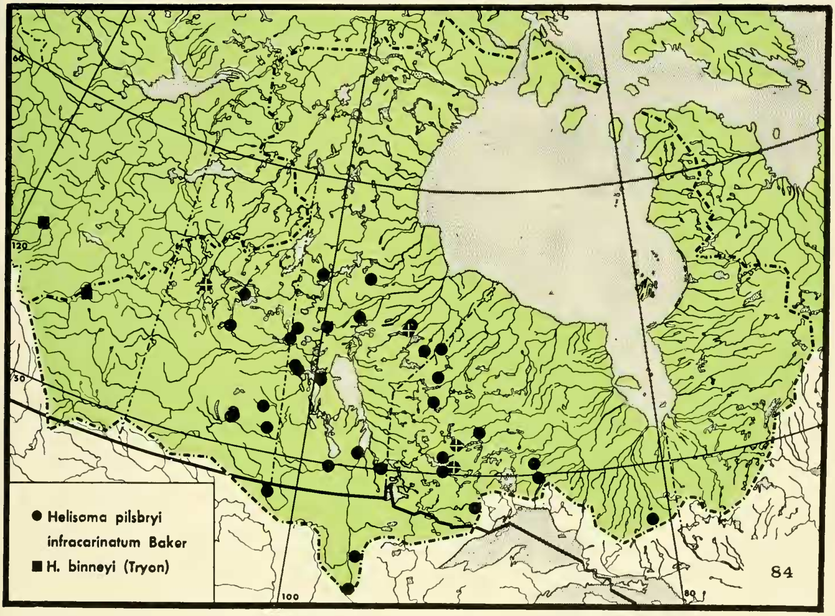
Baker (*loc. cit.*) has also commented on the "perplexing variation" in this subspecies. The variation is so great, in fact, that one is initially tempted to consider it analogous to the variation exhibited by *Gyraulus deflectus* and to regard *Helisoma pilsbryi infracarinatum* as a frequently occurring morphological variant of *H. trivolvis* (Say). All populations show marked variability but nearly all can be wholly assigned to either *H. P. infracarinatum* or *H. trivolvis*. One lot of apparently freshly dead shells from a Lake Winnipeg beach, 20 mi S of Gimli, Man., contains both taxa and they are clearly distinguishable without intermediate forms. Unless they were derived from different source areas, which is possible but unlikely, this find provides some evidence that the taxa are specifically distinct.

It is also possible that *Helisoma pilsbryi infracarinatum* is a morph which is intermediate between *H. corpulentum* (*s. str.*) and *H. trivolvis* (*s. str.*) derived from sporadic introgressive hybridization or representing a surviving parental stock from which *H. corpulentum* arose. The status of *H. p. infracarinatum* as a separate taxon requires additional research.

Other collections of *Helisoma pilsbryi infracarinatum* which are of unusual interest are those from the Qu'Appelle River system, Sask., and from Montreal Lake, Sask., The 6 lots collected from various localities in or near the Qu' Appelle River are quite uniform in being more heavily carinate and much smaller than typical *H. p. infracarinatum*. These plains populations also appear to be geographically isolated from the main series of populations which occupy the forested Precambrian Shield region and may deserve separate subspecific status.

The largest sample of *H. p. infracarinatum* was taken at Montreal Lake, 16 mi N of Waskesiu Lake, Sask. in the Churchill River system (see "Measurements"). All were beach specimens but freshly dead and unusually large. Many exhibit a wide, flaring lip and great axial height. These specimens show marked variation in carination on the left (upper) side, some specimens have rounded early whorls and carinate later whorls, others exhibit an opposite trend, but most are carinate throughout. The lower carina is also variably expressed. This population and other populations from the Churchill River and Hayes River drainage areas appear to differ slightly from populations from the type area but the observed differences do not seem to be sufficiently constant or important to warrant separate taxonomic status. The names *H. kennicotti* Baker and *H. p. preblei* Baker, both of which are available for these populations, are therefore synonymized under *H. p. infracarinatum*.

Remarks on *Helisoma kennicotti*: The correct geographical location of the type locality of *Helisoma kennicotti*, "Lake Isle la Crosse, English River,



Canada " presented a problem. Baker (1936: 22) refers to the USNM lot (No. 29231), later (1945: 223) used as the type lot of *H. kennicotti*, and cites the collector as Robert Kennicott. Kennicott's journal, published by James (1942), shows that Kennicott visited Lac La Crosse on July 24, 1859 on the " English River " (the old name for the middle portion of the Churchill River) while travelling with voyageurs on the route from Lake Winnipeg to Lake Athabasca. There is no lake with a name resembling " Lake Isle La Crosse " on the river in northwestern Ontario which now bears the name " English River " and it is certain that the type locality of *H. kennicotti* is the lake in northern Saskatchewan now called Lac Ile-à-la-Crosse (55°40′N, 107°45′W).

Helisoma (*Pierosoma*) *binneyi*
(Tryon)
Plate 27, Figs. 4-6; Map 84.

Planorbis binneyi Tryon, 1867: *Amer. J. Conchol.*, *3*: 197 (refers to figure 130 in A. A. Gould, 1852, *United States Exploring Expedition*, *12*; to plate 3, figs. 7-9 in S. S. Haldeman, 1844, *Monograph of the Limniades*; and to figs. 191 and 192 in W. G. Binney, 1865, *Land, and Fresh-water shells of North America*). Type locality not specified.

Diagnosis and Description: The specimens from the Canadian Interior Basin confidently identified as *Helisoma binneyi* are carinate and similar to *H. pilsbryi infracarinatum*, except that in *H. binneyi* (1) the body whorl is more expansive, causing the apex and the umbilicus to be much more deeply immersed, (2) the aperture is notably expanded above and below, and (3)

in the lot from Lake Wabamun the specimens are much higher and the whole shell is much larger (see " Measurements").

Measurements:

Max. Dia. mm	Gr. Dia. mm	Gr. Hgt. mm	Gr. Hgt./Gr. Dia.	Riblets/5 mm (in front of aperture)
Wabamun Lake, Seba Beach, Alta.				
28·0	26·1	15·7	0·602	13
27·9	26·8	16·8	0·627	14
25·5	24·2	13·7	0·566	10
20·6	19·8	12·2	0·616	19
McLeod Lake, B.C.				
22·8	22·2	11·8	0·532	19
21·3	20·3	12·1	0·596	15
21·5	19·5	10·6	0·544	18
20·8	19·2	11·4	0·596	23
16·2	15·5	9·1	0·587	19
16·1	15·5	9·0	0·582	20
Clairmont Lake, 2 mi NE of Clairmont, Alta.				
14·7	14·1	7·4	0·525	24
14·4	13·6	7·5	0·551	24
12·7	12·2	6·8	0·557	21
13·5	12·9	6·9	0·535	24
11·9	11·7	6·5	0·556	—*
12·2	11·5	6·7	0·583	25
12·1	11·6	6·7	0·578	36
11·5	11·2	6·6	0·589	—*
10·8	10·6	6·1	0·575	33
10·3	10·0	6·0	0·600	—*
9·8	9·4	5·6	0·596	33
9·6	9·4	5·7	0·606	—*
7·1	6·9	4·3	0·623	—*

* Shell worn or broken so that riblet count not possible.

Records:

Saskatchewan River system. Wabamun Lake, Seba Beach, Alta. (1926, L. S. Russell!).

Mackenzie River system. Peace River drainage area: McLeod Lake, B. C. (1879, G. M. Dawson!). Clairmont Lake, 2 mi NE of Clairmont, Alta. (tentatively referred to *H. binneyi*). (this survey).

Distribution: " West of the Rockies and east of the Cascade Mountains on the Pacific Slope. California, Oregon, and British Columbia. " (La Rocque,

1953: 288). California to British Columbia in the Pacific drainage area and British Columbia and Alberta in the headwaters of the Peace and North Saskatchewan River systems.

Biology and Ecology: There appears to be no detailed published information on the ecology of *Helisoma binneyi*. The records seen from the western United States and Canada are from lakes, however. The specimens from Clairmont Lake, tentatively referred to *H. binneyi* are empty shells from beach drift. Clairmont Lake is large, shallow, and eutrophic.

The anatomy of this species has not been investigated. Baker (1945: 142-148) has described the anatomy of *Helisoma traskii* (Lea) which may be closely related to *H. binneyi*, and gives the radula formula of *H. traskii* as 28-1-28 to 30-1-30.

Remarks: Henderson (1934) has published the most informative discussion of western planorbids which has appeared. His approach is typological, however, and it is most difficult to decide which of the nominate species most closely matches the material now at hand. The Wabamun Lake specimens bear similarities to Henderson's figures of both *H. binneyi* and *H. ammon* (Gould). The McLeod Lake specimens are like the figures of *H. binneyi* and the Clairmont Lake specimens are closer to the figures of *H. occidentale* Cooper. (Several of the Clairmont Lake specimens have a prominent and vivid blue band inside the aperture.) The figures of western *Helisoma* published by Baker (1945, pl. 93-95) do not solve the problem.

The name *Helisoma binneyi* is used here for convenience. *H. binneyi*, *H. ammon*, *H. occidentale*, and *H. traskii* are all closely related and may be found to belong to 1 species when the problem is investigated thoroughly.

30

It is of some interest here that a typical specimen of *Helisoma trivolvis subcrenatum* was collected along with the *H. binneyi* here reported from Wabamun Lake. Of course more material is needed but the occurrence of both taxa together implies that they are specifically distinct.

Helisoma (*Pierosoma*) *corpulentum corpulentum* (Say)
Plate 27, Figs. 7-9; Map 85.

Planorbis corpulentus Say, 1824: *Major Long's Second Exped. to the Source of St. Peter's River*, [etc.], *2*: 262, pl. 15, fig. 9. (Binney reprint, 1858: 128, pl. 74, fig. 9). Type locality: " Winnipeck River, Winnipeck Lake, Lake of the Woods, and Rainy Lake. "

Helisoma corpulentum multicostatum F. C. Baker, 1932: *Nautilus*, *46*(1): 7. Type locality: " Kahnipiminanikok [Kawnipi] Lake, Rainy River District, western Ontario, Canada. "

Diagnosis: Shell large, planorboid, sinistral, proportionately high, abaxially carinate above and abaxially subcarinate below, spire flat or concave, and with the outer side of the body whorl flattened.

Description: Shell large (up to about $1\frac{1}{4}$ inches in diameter), planorbiform, with up to $4\frac{1}{2}$ whorls, sinistral, light brown to dark brown, sharply carinate above and with a slightly flattened body whorl. Apical (left) side flat or slightly concave and, in most specimens, sunken below the enveloping body whorl. Apical carina sharp and forming a right angle on all early whorls but becoming more or less rounded on the last half of the body whorl. Apical carina located near abaxial edge on early whorls and there forming a sharp shoulder, but becoming centrally located on the body whorl. Umbilical carina even sharper on the early whorls but, on many specimens, becoming rounded on the body whorl and shifting to an abaxial location. Body whorl flattened, especially on the

PLATE 27. Planorbidae (III)

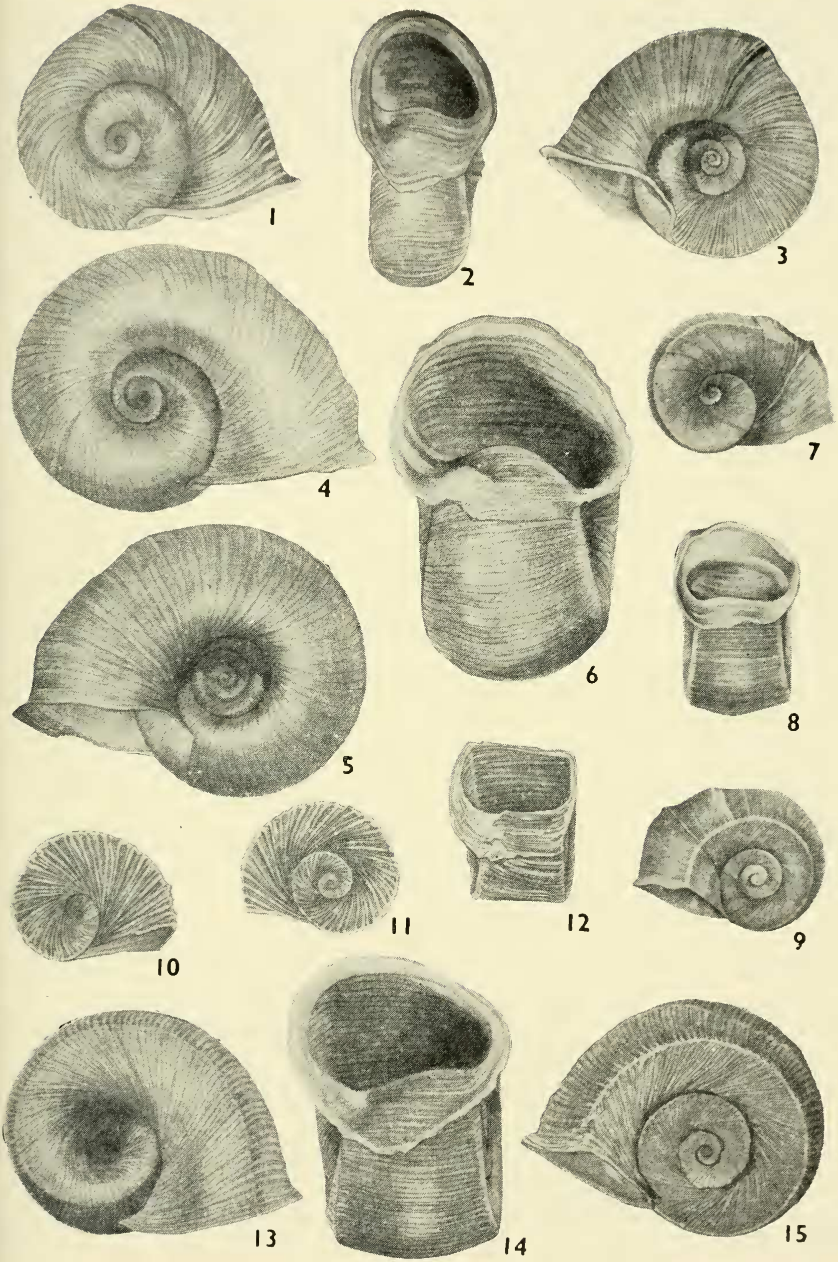
FIGS. 1–3. *Helisoma trivolvis trivolvis* (lectotype of *Planorbis macrostomum* Whiteaves), Montreal. Quebec (NMC 3869, 23 mm) . . . . p 452

FIGS. 4–6. *Helisoma binneyi*, Wabamun Lake, Alberta (NMC 12267, 28 mm) . . . . p 463

FIGS. 7–9. *Helisoma corpulentum corpulentum*, Lac Seul, Ontario (NMC 11480, 15·5 mm) . . . . p 465

FIGS. 10–12. *Helisoma corpulentum vermilionense*, Vermilion Lake, Minnesota (NMC 3220, 14 mm) . . . . p 471

FIGS. 13–15. *Helisoma corpulentum whiteavesi*, Lac des Mille Lacs, Ontario (NMC 3223, 24 mm) . . . . p 472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upper surface of its outer side and in many specimens on the base. In some specimens the body whorl is also bent upward near the aperture. Aperture large, expanded, higher than wide, and extending only above or both above and below the body whorl. Umbilicus wide, deep, and exhibiting the apical whorls. Sculpture strong and consisting of prominent, crowded, strongly elevated, collabral riblets (see " Remarks ") and microscopic collabral and spiral striae.

Measurements:

Feature	N	Range	Mean	$S.E._M$	S.D.
Pelican Lake, Sioux Lookout, Ont.					
Max. Dia., mm	8	18·2 —22·0	20·41	—	—
Gr. Dia., mm	8	16·8 —21·6	19·44	—	—
Gr. Hgt., mm	8	9·1 —11·0	10·64	—	—
Gr. Hgt./Gr. Dia.	8	0·509— 0·603	0·546	0·011	0·030
Riblets/5 mm *	8	7·5 —13·0	10·9	0·6	1·7
Wabaskang Lake, 40 mi N of Vermilion Bay, Ont.					
Max. Dia., mm	11	21·0 —26·1	23·89	—	—
Gr. Dia., mm	11	19·5 —22·9	22·13	—	—
Gr. Hgt., mm	11	11·1 —13·0	11·72	—	—
Gr. Hgt./Gr. Dia.	11	0·486— 0·633	0·572	0·012	0·040
Riblets/5 mm *	11	11·5 —18·0	14·4	0·5	1·7
Lake of the Woods, Kenora, Ont.					
Max. Dia., mm	26	16·1 —21·9	18·92	—	—
Gr. Dia., mm	26	15·2 —20·2	17·59	—	—
Gr. Hgt., mm	26	9·3 —13·4	12·01	—	—
Gr. Hgt./Gr. Dia.	26	0·544— 0·731	0·625	0·009	0·044
Riblets/5 mm *	18	8·5 —15·0	10·8	0·4	1·5

* Measured immediately in front of aperture.

Records:

Winnipeg River system. Rainy River-Lake of the Woods drainage area: Lac de Mille Lacs swamp, Basswood River Rapids, Kawnipi [" Kahnipiminanikok "] Lake, Sturgeon River, Birch Lake, and Lac la Croix, all Rainy River District, Ont.; Iron Lake, Ont. -Minn. International Boundary; and Fall Lake, near Ely, Minn. (all 1928, 1931, A. R. Cahn!). One-Sided Lake [Caliper Lake], approx. 60 mi SE of Kenora, Ont., Golf Course Bay, Lake of the Woods, Kenora (both this survey). Lake of the Woods (1882, J. Fletcher!). Kenora [" Rat Portage "], " just above falls " (1884, A. C. Lawson!). English River drainage area: South end, Lake St. Joseph, Ont. (1929, A. R. Cahn!). Paguchi Lake, 7 mi N of Ignace, Ont. Nugget Creek, 12 mi E of Dryden, Ont. Inlet of small lake 3 mi W of Patricia, Ont. Pelican Lake, Sioux Lookout, Ont. Frog Rapids, Abram Lake, Sioux Lookout. Sturgeon River [Marchington River], 1 mi W of Superior Junction. Ont. (all this survey). Abram Lake (1929, A.R. Cahn!). Minnitaki Lake, Sioux Lookout [" Sioux Outlook "], and Root River, Ont.

(all 1904, W. McInnes!). English River below Manitou Falls, Ont. (1905, W. McInnes!). Lac Seul, Ont. (1904, W. McInnes! and 1919, F. W. Waugh!). Chukuni River, 2 mi E of Red Lake, Ont. Red Lake, Rahill Beach, Cochenour, Ont. Moth Lake, 25 mi W of Kenora, Ont. (all this survey). Lake 3 mi E of Falcon Lake, Man. (1962, F. R. Cook and C. B. Powell!).

Distribution: Western Ontario, eastern Manitoba and northern Minnesota in the Winnipeg River system. Also in the upper Mississipi River system in northern Minnesota (Baker, 1936: 7 and this survey). Mozley's (1938: 106) statement " Confined to the forested region " is confirmed.

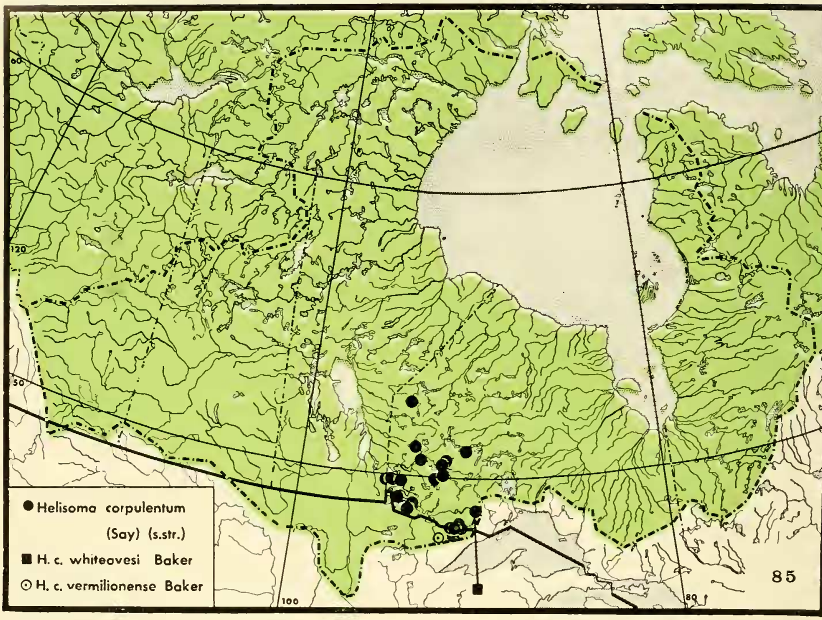
Biology and Ecology: Eleven lots of *Helisoma corpulentum corpulentum* were collected during this survey. Four of these are from large lakes, 3 are from small lakes, and 4 are from rivers over 100 feet in width. Vegetation varied from sparse to thick, bottom deposits were of all sorts (clay, mud, sand, gravel, or rocks, or any combination of these) and current in the river habitats was appreciable in all cases, varying from slow to moderately rapid.

Microhabitat observations were not made at all localities. Some collections in fact were of empty shells from windrows but in general it appears that *Helisoma corpulentum corpulentum* occupies more exposed situations than does *H. trivolvis trivolvis*. At Pelican Lake, Sioux Lookout, Ont., for example, both species were taken from significantly different habitats. *H. c. corpulentum* was found only on semi-exposed rocks while *H. trivolvis* was taken only from among reeds in muddy coves. Grant (1887, quoted by Walker, 1900: 135) says: " it is found clinging to rocky shores and reefs, and seems to seek places where the water is quite rough. " Present observations indicate that Grant's statement is correct but that more protected situations are also inhabited. In this respect *H. c. corpulentum* is much like *Lymnaea catascopium* morph *emarginata*.

The anatomy of *Helisoma corpulentum corpulentum* has been discussed by Baker (1945: 139, 148, etc.). It is similar to that of *H. trivolvis trivolvis* but differs in details of the genitalia and in the number of radula teeth in each transverse row. Baker gives the radula formula of *H. c. corpulentum* and of *H. c.* " *multicostatum* " as varying from 32-1-32 to 45-1-45 in adult individuals from various localities. Radula preparations from adult specimens collected during the present survey give formulae as follows:

Locality	Cat. No.	Max. Dia., mm	Radula Formula
Frog Rapids, Sioux Lookout, Ont.	25664 B	17·4	$\frac{19}{4\text{–}6}-\frac{13}{3}-\frac{1}{2}-\frac{13}{3}-\frac{18}{4\text{–}6}$ (32–1–31)
Nugget Creek near Dryden, Ont.	26212 B	22·6	$\frac{17}{4\text{–}6}-\frac{13}{3\text{–}4}-\frac{1}{2}-\frac{13}{3\text{–}4}-\frac{16}{4\text{–}6}$ (30–1–29)
Nugget Creek near Dryden, Ont.	26212 C	21·0	$\frac{14}{4\text{–}6}-\frac{13}{3}-\frac{1}{2}-\frac{13}{3}-\frac{13}{4\text{–}6}$ (27–1–25)
Nugget Creek near Dryden, Ont.	26212 D*	22·1	$\frac{17}{4\text{–}6}-\frac{13}{3}-\frac{1}{2}-\frac{13}{3}-\frac{16}{4\text{–}6}$ (30–1–29)

26212 D has lateral teeth with 4 cusps in some transverse rows.



Remarks: *Planorbis corpulentus* Say was regarded as a synonym of *P. trivolvis* by nearly all malacologists until Walker (1900) pointed out its true relationships. Baker (1932, 1936) discussed the status of the various northern forms of *Helisoma corpulentum* and *H. trivolvis* and based on abundant material collected by A. R. Cahn in northwestern Ontario in 1928, 1929, 1931, and 1935, he described several new " races " and related species. In the *H. corpulentum* group *H. c. vermilionense*, *H. c. multicostatum*, and *H. whiteavesi* were described.

The status of *Helisoma corpulentum* as a separate species is, I think, secure. It is morphologically very different from *H. trivolvis*, it occupies a discrete geographical area within the overall range of *H. trivolvis*, it exhibits marked ecological differences as compared with *H. trivolvis*, and when found in the same water body the 2 species are readily separable without intergrades. During this survey such mixed assemblages occurred at Pelican Lake, Sioux Lookout, Ont. and at Golf Course Bay, Lake of the Woods, Kenora, Ont. Mixed assemblages were also seen by Baker & Cahn (1931: 56) from Bamaji and St. Joseph lakes, Ont. See also " Remarks " under *H. pilsbryi infracarinatum*.

The status of the related taxa listed above needs examination, however. Both *Helisoma corpulentum vermilionense* and *H. whiteavesi* are poorly represented in collections but appear to be morphologically distinct and to occupy discrete geographical subregions. Although study of more material might alter their separate status there is now no proper basis for refusing to recognize them taxonomically and they are both

here retained as subspecies of *H. corpulentum*.

Helisoma corpulentum multicostatum cannot be retained. The characteristics listed by Baker as diagnostic (finer and more crowded riblets, persistence of the basal carina on the edge of the body whorl, and more whorls visible on the base) are variable and all variations occur throughout the whole geographical range of *H. corpulentum* (*s. str.*). Riblet spacing on the body whorl was considered the chief diagnostic feature of this " variety " by Baker, who quotes 1 riblet per mm for *H. corpulentum* (*s. str.*) and 3 to 4 riblets per mm for *H. c.* " *multicostatum* ". Several population samples were examined for riblet spacing by counting the riblets in a 5 mm long area just in front of the aperture. Results for the 3 largest samples are given under " Measurements, " and smaller samples give similar results. It can be seen that when riblet counts are taken in this manner values vary from approximately $1\frac{1}{2}$ to $3\frac{1}{2}$ riblets per mm and in single samples variations of approximately $1\frac{1}{2}$ riblets per mm were normal. Since the geographical ranges of both *H. corpulentum* (*s. str.*) and *H. c.* " *multicostatum* " are also concordant (Baker, 1936: 10), the 2 morphs cannot be considered as other than taxonomically identical.

Helisoma (*Pierosoma*) *corpulentum vermilionense* Baker

Plate 27, Figs. 10-12; Map 85.

Helisoma corpulenta vermilionensis Baker, 1929: *Nautilus 42*(4): 131-132. Type locality: " Birch Point, Big Bay, Vermilion Lake, St. Louis Co., Minn. "

Diagnosis and Description: " Shell differing from typical *corpulenta* in having the whorls at the shoulder and base encircled by a sharp, cord-like carina which persists in the aperture both above and below, the spire is much flatter, the umbilicus much flatter and relatively deeper with the penultimate whorl sunk below the last whorl to a greater extent than in the typical form; the axial height is greater and the aperture is longer and narrower and peculiarly effuse and expanded below; the body whorl is much more flat-sided in the variety, hence profoundly modifying the aperture in form. " (Baker, 1929: 131-132). " In most specimens the new whorl is so tightly appressed to the preceding whorl as to form a marked plait on the columella, which is notably conspicuous on immature shells. The sculpture of the surface is usually coarse like that of the typical form, but specimens occur with the fine sculpture of *multicostatum*. " (Baker, 1936: 7).

Measurements* :

Diameter, mm	Height, mm	Hgt./Dia.	Aperture Dia., mm	Aperture Hgt., mm
Vermilion Lake, Minn. (Type lot).				
21·5	15·0	0·698	12·0	16·0
22·0	14·0	0·637	12·0	15·5
17·5	13·5	0·772	9·5	13·0
13·5	12·0	0·889	9·0	11·0
13·5	13·0	0·963	7·0	11·7
10·0	8·0	0·800	5·5	7·9
7·0	6·5	0·929	4·0	6·5

* Except for the ratio Hgt./Dia. the measurements are from Baker (1929: 132). " L " and " Ap. L." in Baker are here referred to as diameter and aperture diameter.

Records:

Winnipeg River system. Vermilion Lake, St Louis Co., Minnesota (1928, F. C. Baker!) Paratypes of *H. c. vermilionense*.

Distribution: Known only from the type locality.

Biology and Ecology: "This variety of *corpulenta* occurs abundantly in Lake Vermilion on more or less exposed shores, in shallow water, on shingle or cobble bottom. In many places the bottom is fairly peppered with the shells. In the aquarium the animal crawls about with a rapid, gliding motion, examining objects with its long, filiform tentacles." (Baker, 1929: 132).

The reproductive anatomy of this subspecies is similar to that of the nominate subspecies (Baker, 1945: 139). Radula formulae are 30-1-30 to 31-1-31 (mature) and 25-1-25 to 27-1-27 (immature) (Baker, 1945: 148).

Remarks: Eight paratypes of *Helisoma corpulentum vermilionense* are in the National Museum of Natural Sciences. These are all immature specimens of 2½ to 3 whorls but all differ from typical *H. corpulentum* in having strong, acutely angled carinae above and below and in having the outer (abaxial) surface of the first 2½ whorls markedly concave.

Although no other lots are available it is significant that the 1 lot of *Helisoma corpulentum corpulentum* which most resembles *H. c. vermilionense* is from the locality closest to Vermilion Lake represented by specimens. This lot is from Iron Lake, St. Louis County, Minnesota, collected by A. R. Cahn in 1931. Vermilion River drains Vermilion Lake and flows into Iron Lake. The specimens are similar to *H. c. vermilionense* except that the whorls are slightly convex and the carinae are not quite as strong as in Vermilion Lake specimens.

Helisoma (*Pierosoma*) *corpulentum whiteavesi* Baker

Plate 27, Figs. 13-15; Map 85.

Helisoma whiteavesi F. C. Baker, 1932: *Nautilus*, *46*(1): 7-8. Type locality: "Lac des Mille Lacs, Thunder Bay District, western Ontario, Canada".

Diagnosis and Description: "This species may be recognized by the great axial height of the body whorl at the aperture, the flat, almost truncated spire surface, the fine striae, finer than in *multicostatum*, the flatly-rounded base showing barely 2 whorls, and the large ear-shaped aperture, which gives the shell a physoid aspect." (Baker, 1932: 7).

Measurements* :

No.	Gr. Dia., mm	Gr. Hgt., mm	Gr. Hgt./Gr. Dia.	Ap. Dia., mm	Ap. Hgt., mm
1	24·0	19·0	0·792	9·0	15·5
2	23·2	18·2	0·785	9·0	15·0
3	21·5	16·8	0·781	8·1	14·2
4	10·4	12·0	1·154	5·0	11·2
5	24·5	14·4	0·588	9·3	15·0
6	23·0	15·0	0·652	10·0	16·0

* Measurements of specimens 1–4 are from the type lot and are quoted from Baker (1932: 8). Measurements of specimens 5 and 6 are from paratype specimens in the National Museum of Natural Sciences (Cat. No. 3223). The ratio Hgt./Gr. Dia., has been added here for comparative purposes.

Records:

Winnipeg River system. Greenwater Lake, Thunder Bay District, Ont. (48°35′N, 90°25′W) (1890, W. McInnes!). Lac des Mille Lacs, Thunder Bay District, Ont. (paratypes of *H. whiteavesi*) (1928, A. R. Cahn!).

Distribution: Known only from the 2 localities cited above. These lakes are about 15 miles apart and drain into the headwaters of the Rainy River.

Biology and Ecology: This subspecies is apparently found in an open lake habitat at the type locality, if we can judge from a lot of *Helisoma corpulentum* (*s. str.*) also collected by A. R. Cahn in 1928 labelled " Lac des Mille Lacs swamp. " Otherwise nothing is known about its ecology. An effort to collect it in Lac des Mille Lacs in 1969 proved fruitless.

The reproductive anatomy of *Helisoma corpulentum whiteavesi* has been described by Baker (1945: 139). It resembles that of *H. corpulentum* (*s. str.*). The radula formula is quoted (Baker, 1945: 148) as 36-1-36 to 42-1-42.

Remarks: Baker (1936: 11) states that " the sculpture is coarser than in the race *multicostatum*, but finer than in typical *corpulentum*. " Originally, however, he described the sculpture as finer than " *multicostatum* " (see above). Two paratypes in the National Museum of Natural Sciences show 14 and 16 riblets in a 5 mm long area immediately in front of the aperture. This agrees with the finely sculptured morph now considered as *Helisoma corpulentum* (*s. str.*).

The subspecific status of *H. c. whiteavesi* should be re-examined based on more material from the type area and surrounding regions. The Green Lake specimens are rather like *H. corpulentum* (*s. str.*) but are still referable to *H. c. whiteavesi* in my opinion and in the opinion of Baker (1936: 11). This apparently indicates that there is some gene exchange between *H. c. whiteavesi* and *H. c. corpulentum* and that its status as a subspecies is probably correct.

Family ANCYLIDAE Rafinesque

Ancylidia Rafinesque, 1815: *Analyse de la Nature*, p 143. Binney & Tryon (1864) reprint, p 17. Corrected to Ancylinae by P. H. Fischer, 1883, *Man. Conchyliol.*, p 504. Type genus: *Ancylus* Geoffrey (=*Ancylus* Müller, 1774). The subfamily name Ancylinae has been placed on the Official List of Family-Group Names in Zoology (Name No. 78) by Direction 41 of the International Commission on Zoological Nomenclature, 1956.

Shells patelliform, small to medium-sized and thin to somewhat thickened; with rounded to elongate-ovate aperture; with radial and concentric sculpturing variously developed; and with an apex which may be low or elevated and which is located centrally or posteriorly and on the mid-line or to the right. Radula formulae vary from about 8-1-8 (some *Rhodacmea*) to about 37-1-37 (*Ancylus*). The central tooth has 2 or 4 cusps and the laterals and marginals have 2 to many cusps (Hubendick, 1963).

The soft parts are sinistrally organized with the mantle opening, genital pore, anus, and pseudobranch on the left side, as in other higher Basommatophora. The Ancylidae are most closely related to the Planorbidae, from which they may have been derived. For details of the comparative anatomy of the groups within Ancylidae see Hubendick (1963) and for the anatomy of North American species see Basch (1963a).

According to Hubendick (1964: 62, 68), whose arrangement is followed here, the Ancylidae are a world-wide family containing 7 well-characterized genera. These are *Ancylastrum* Bourguignat, *Ancylus* Müller, *Burnupia* Walker, *Ferrissia*

Walker, *Gundlachia* Pfeiffer, *Laevapex* Walker, and *Rhodacmea* Walker, with *Amphigyra* Pilsbry and *Neoplanorbis* Pilsbry (both endemic to the Coosa River in Alabama and probably now extinct) in a separate, related group of uncertain status. Subfamily categories are not used by Hubendick and phylogenetic relationships between genera are still unclear.

Ancylidae have been recorded from the Middle Oligocene to the Recent. Only the genera *Laevapex* and *Ferrissia* are still living in boreal North America.

KEY TO SPECIES OF ANCYLIDAE

1. Shell depressed, thin, and with ovate aperture. Apex without microscopic radial striae. Epithelial attachment areas, visible through shell, located between the anterior muscle attachments and between the right anterior and the posterior muscle attachments. Penis, when present, large. In standing water. Ontario (rare) and south . . . . *Laevapex fuscus* (p 474, Pl. 28, Figs. 5, 6).
   Shell elevated or depressed, thin to slightly. thickened, and with aperture ovate or with straight, parallel sides. Apex with microscopic radial striae. Epithelial attachments absent between muscle attachments. Penis, when present, small. In standing or running water. Widely distributed and common (*Ferrissia* spp) . . . . 2.
2. Aperture with straight, parelle1 sides. Habitat in standing water . . . . *Ferrissia parallela* (p 481, Pl. 28, Figs. 9, 10).
   Aperture ovate, sides curved and not parallel. Habitat in running water . . . . *Ferrissia rivularis* (p 479, Pl. 11, Figs. 2, 3; Pl. 28, Figs. 7, 8).

Genus *Laevapex* Walker

Laevapex Walker, 1903: Notes on eastern American ancyli. *Nautilus, 17*(2) : 15 (as section of *Ancylus*). Type species: *Ancylus fuscus* Adams, by original designation.

Shell limpet-like, up to 8 mm long, thin, and without radial striations on the apex. Apex depressed, obtuse, and located behind the centre and almost in the midline of the shell. The horizontal septum seen in some specimens of *Ferrissia* is absent in all specimens of *Laevapex*. Penis large when present and without a flagellum. Pseudobranch of 2 lobes, the lower of which is elaborately folded. Radula similar to that of *Ferrissia*. Epithelial attachment areas (visible through the cleaned shell) located between the areas of muscle attachment (see under *L. fuscus*).

According to Basch (1963a: 418) *Laevapex* contains only 2 species. *L. fuscus* is widespread in eastern North America and *L. diaphanus* (Haldeman) occurs only in the southeastern and east-central United States. Geologic age: Pleistocene (Sangamon: Hibbard & Taylor, 1960: 49), to Recent.

Laevapex fuscus (Adams)
Plate 28, Figs. 5, 6; Map 86.

Ancylus fuscus C. B. Adams, 1841: *Descriptions of thirteen* [*sic*. eleven] *new species of New England shells. Boston J. natr. Hist., 3*: 329, pl. 3: 17. Type locality: " adhering to stones, in a small rivulet, at Andover [Massachusetts]....It has also been found at Mansfield [Massachusetts]. "

Diagnosis: Shell about $\frac{1}{3}$ inch long, ovate, depressed, smooth or with fine raised riblets, especially anteriorly. Apex smooth. Epithelial attachment areas visible between muscle attachments (see " Remarks ").

Description: " *Shell* thin, transparent without the epidermis, not much elevated, elliptical, moderately curved at the sides; *epidermis* brown, visible through the shell, giving it the appearance of having the same color, thick, rough, slightly extending beyond the margin of the shell; *apex* obtuse, moderately prominent, scarcely behind the middle. inclining to the right, so as to have only two-fifths of the width on that side. Length, 0·31 inch; width, 0·22 inch; height, 0·05 inch. " (Adams, loc. cit.).

Measurements:

Locality	N	Mean L mm	Mean W mm	Mean H mm	L/W	L/H	W/H
Andover, Mass. (holotype)*	1	7·87	5·59	1·27	1·4	6·2	4·4
Ottawa Co., Mich.*	1	8·25	4·5	3·0	1·8	2·8	1·5
Geddes Bridge, Mich.*	25	5·34	3·75	1·72	1·4	3·1	2·2
Greenbriar Co., W. Va.*	36	4·45	3·49	1·45	1·3	3·1	2·4
Medcalfe Lake, Ont.	1	4·0	2·4	1·3	1·7	3·1	1·8

* All measurements except those for the Medcalfe Lake specimen are from Basch (1959 : 12).

Records:

Albany River system. Bamaji Lake, Ont. (Baker & Cahn, 1931: 60). Medcalfe Lake, north end, 63 mi N of Savant Lake, Ont. (one living and one empty and broken shell, this survey).

Distribution: Central Ontario south to Florida and Louisiana and (according to literature records quoted by Basch, 1963a: 420) west to Iowa, Kansas, and Oklahoma.

Biology and Ecology: Medcalfe Lake, the single locality for *Laevapex fuscus* discovered during this survey, is large, eutrophic, and contains many species of molluscs. The area was searched briefly at dusk on August 8, 1961. Vegetation was thick, bottom sediments were of sand and muddy sand, and collections were made chiefly by sweeping the submersed parts of aquatic vegetation with a dip net near the shore in depths down to about 3 feet.

Basch (1963a: 470) gives backwater areas of rivers and densely-vegetated portions of lakes and slow-flowing rivers as the characteristic habitats of this species. In such situations it occurs " on the undersides of lily pads, on cat-tails, sedges, and other emergent rooted vegetation. Rarely, this species may be found together with *Ferrissia rivularis* when in a stream, or with *F. fragilis* when in a stagnant pool " (Basch, loc. cit.). In Medcalfe Lake it was found associated with *Lymnaea stagnalis appressa*, *Helisoma anceps royalense*, *Gyraulus deflectus*, *Amnicola limosa*, and *Valvata tricarinata*.

Basch (1959) has described the anatomy of *Laevapex fuscus* in excellent detail. The genitalia are sharply different from those in other freshwater limpets but the radula is similar to that of *Ferrissia* and of *Hebetancylus*, a subtropical and tropical American genus. The reproductive system is relatively large implying that *L. fuscus* may lay more eggs than other ancylids but this needs to be confirmed by observation.

Remarks: The most useful external characters for distinguishing *Laevapex fuscus* from *Ferrissia* species are as given below. All these characters are much more visible in specimens which are well cleaned and which have had the periostracum removed with a weak solution of laundry bleach in water. (1) A prominent, dorsal band of dark pigment located on the mantle near the middle may be seen through the shell of *L. fuscus*. A similar band is almost never seen in *Ferrissia*, although dark colouring near the edge of the mantle is visible in both *Laevapex* and *Ferrissia*. The tentacles of *L. fuscus* also have a black core and those of *Ferrissia* spp. do not. (2) As pointed out by Burch (1963: 9), in *Laevapex* " there are usually three main muscle scars, one each on the anterior right and left sides and one

PLATE 28. Acroloxidae and Ancylidae

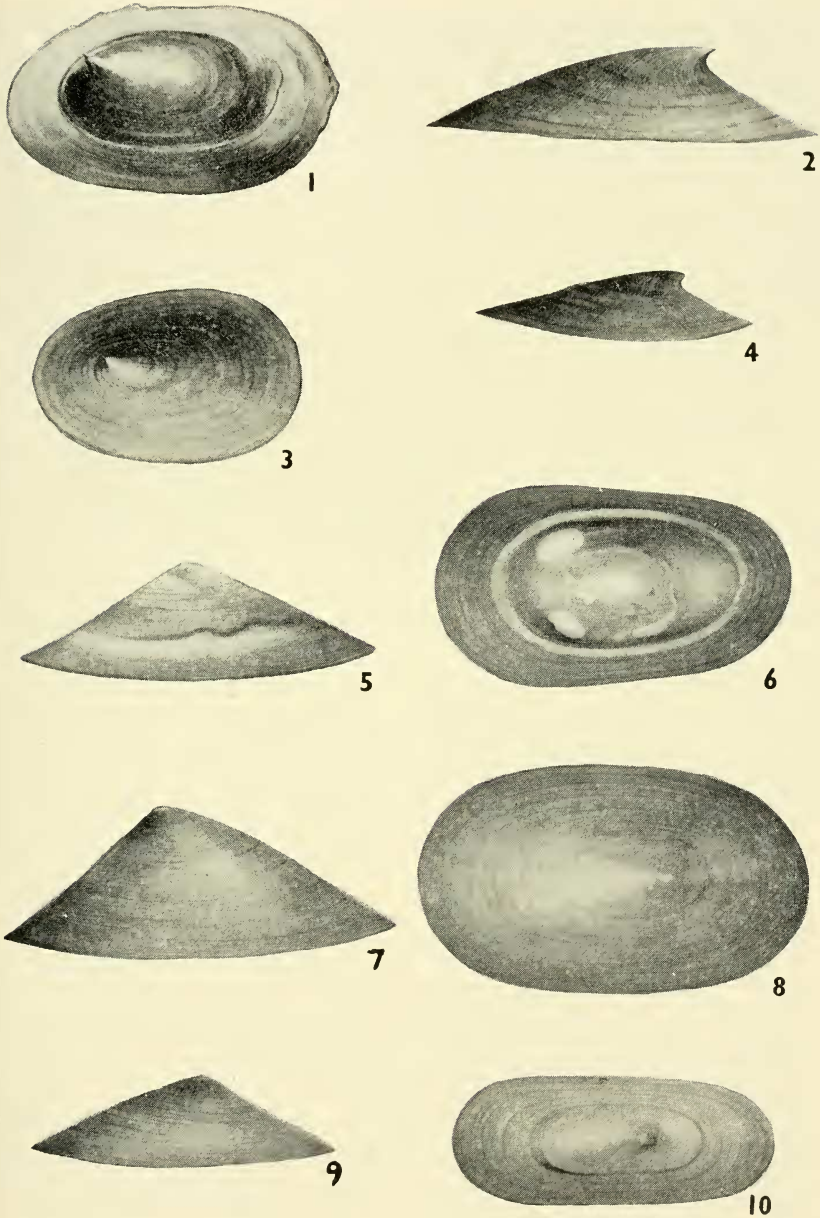
FIGS. 1, 2. *Acroloxus coloradensis*, Lac Gabrielle, near Chibougamau, Quebec (NMC 22323, 4·7 mm). . . . . p 262

FIGS. 3, 4. *Acroloxus coloradensis*, Lake No. 1, N of Geikie Station, Alberta. (ANSP 152666, 2·9 mm). . . . . p 262

FIGS. 5, 6. *Laevapex fuscus* (periostracum removed to show muscle and epithelial attachments) N end of Medcalfe Lake, 63 mi N of Savant Lake, Ontario. (NMC 19539, 3·9 mm). . . . . p 474

FIGS. 7, 8. *Ferrissia rivularis* Whitesand River near Sheho, Saskatchewan. (NMC 32320, 4·3 mm). . . . . p 479

FIGS. 9, 10. *Ferrissia parallela*, Klotz Lake, Ontario (NMC 22321, 6·9 mm). . . . . p 481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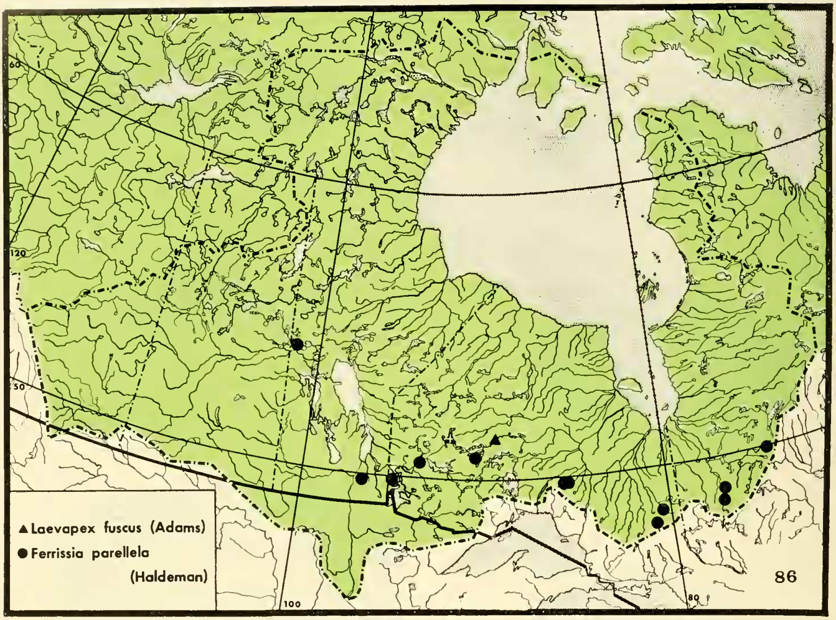


on the left posterior side. Between the two anterior muscle scars and the right anterior and the posterior muscle scars there are smaller, usually broken areas of adhesive epithelium. In *Ferrissia*... the broken areas of adhesive epithelium are lacking." See Pl. 11, Figs 2, 3. (3) In *Ferrissia* the apex is sculptured with numerous, fine, radial lines; in *Laevapex* the apex is smooth. Magnifications of 60x and higher are necessary in order to observe clearly this fine apical sculpturing. The sides of the shells of both genera may bear radial lines but these begin below the apex.

Empty and bleached specimens of freshwater limpets are also available from localities in the Mackenzie River system, viz., Pembina River near Sangudo, Alta. (1926, L. S. Russell !); Trout Creek, 14 mi NE of Edson, Alta. (1965, H. D. Athearn!); Hay River mouth at Great Slave Lake (1944, J. G. Oughton !; also 1966, R. W. Coleman and J. Ferguson !); and Big Buffalo River mouth at Great Slave Lake (1944, J. G. Oughton !). Some of these specimens show internal muscle and epithelial attachment scars which are in the same position as the muscle and epithelial attachments in *Laevapex fuscus*. The Big Buffalo River specimens even appear to have traces of dried tissue within. It is possible that *L. fuscus* or another species of *Laevapex* lives in that region, but until live-collected material is available no decision should be made.

Genus *Ferrissia* Walker

Ferrissia Walker, 1903: Notes on eastern American ancyli. *Nautilus*, *17*(2): 15 (as section of *Ancylus*). Type species: *Ancylus rivularis* Say, by original designation.

Shell limpet-like, up to 10 mm long, moderately thick to thin, and with microscopic radial striations on the apex. Apex elevated or depressed, obtuse and located behind the centre and in the midline or to the right of midline. A horizontal shelf-like septum (rather similar to that in *Crepidula*) is present in some specimens from more southern localities. Penis small (when present) and with a club-shaped flagellum. Pseudobranch flat and of one lobe. The central tooth of radula with 2 equal mesocones and 2 minute ectocones and the lateral and marginal teeth are multicuspid. There are no epithelial attachment areas on the shell between the areas of muscle attachments.

The genus *Ferrissia* is world-wide (except apparently absent from South America) and probably contains approximately 30 species, although no comprehensive revision has been made which would allow an accurate estimate. Geologic age: Eocene to Recent (Zilch, 1959: 127).

Ferrissia rivularis (Say)

Plate 11, Figs. 2, 3, 7; Pl. 28, Figs. 7, 8; Map 87.

Ancylus rivularis Say, 1817: *J. Acad. natr. Sci. Philad., 1*: 125 (Binney reprint, 1858: 60). Type locality not specified, but Haldeman's (1844, pt. 7: 5) statement " the Delaware and Susquehanna " has been accepted by subsequent authors as the type locality.

Ancylus tardus Say, 1831 (Jan. 15): *N. Harmony Dissem. useful Knowl.*, (Binney reprint 1858: 149). Type locality: " inhabits the Wabash River. "

Ancylus ovalis Morse, 1864: *J. Portland Soc. natr. Hist., 1*: 44, text figs. 101, 102. Type locality: " Androscoggin River at Bethel, Me. "

Ancylus borealis Morse, 1864: op. cit., p 45, text figs. 103, 104. Type locality: " Patten, in the northern part of the State [Maine]. "

Diagnosis: Shell up to about $\frac{1}{4}$ inch long, elliptical, elevated, relatively smooth and aperture with rounded, convex sides. Apex obtuse, in the midline or slightly to the right, and very finely striate.

Description: " Ovate, the margins regularly curving, the ends rounded; anterior slope convex, posterior slope concave below the apex but more or less straight near the peritreme; right slope slightly convex or straight; left slope usually straight but sometimes slightly convex; shell rather well elevated, with a subacute apex, inclining somewhat toward the right side; the apex is situated about a third of the distance from the posterior end; apex radially striate; growth lines somewhat irregular, well marked, with more or less of radial sculpture on the anterior slope; the peritreme of the shell is usually quite flat; the greatest width of the shell is in front of the apex, the shell narrowing somewhat posteriorly; color pale corneous. " (Baker, 1928a: 398).

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Crane Lake, Man.					
Length, mm	11	4·1—6·9	5·15	—	—
Width, mm	11	2·4—3·9	3·10	—	—
Height, mm	11	1·7—2·9	2·20	—	—
L/W	11	1·6—1·8	1·66	0·02	0·05
L/H	11	2·2—2·6	2·38	0·05	0·16
W/H	11	1·3—1·6	1·43	0·03	0·10

Feature	N	Range	Mean	$S.E._M$	S.D.
Rat River, 1½ mi S of La Rochelle, Man.					
Length, mm	15	3·6—5·0	4·22	—	—
Width, mm	15	2·2—3·0	2·56	—	—
Height, mm	15	1·4—1·7	1·67	—	—
L/W	15	1·6—1·7	1·69	0·01	0·05
L/H	15	2·1—3·0	2·52	0·07	0·26
W/H	15	1·2—1·8	1·48	0·04	0·15

Records:

Albany River system. Stooping River mouth, 12 mi W of Fort Albany, Ont. Side channel of Albany River, 9 mi W of Fort Albany (both this survey).

Attawapiskat River system. Monument Channel, 6 mi W of Attawapiskat, Ont. (this survey).

Winnipeg River system. Whitemouth River, Whitemouth, Man. (this survey).

Red River system. Red River, 2 mi NE of Drayton, N. D. Roseau River, 8 mi N of Tolstoi, Man. Rat River, 1½ mi S of La Rochelle, Man. Seine River, Grande Pointe, Man. Whitesand River, 9 mi ESE of Sheho, Sask. (all this survey). Birdtail Creek, Birtle, Man. (Mozley, 1938: 114). Minnedosa River, 10 mi NNW of Minnedosa, Man. (this survey).

Lake Manitoba-Lake Winnipegosis drainage areas. Crane Lake, Man. (1894, J. Macoun!). Whitemud River, Gladstone, Man. (this survey). Kipabiskau Lake, Sask. (date, collector?). Valley River, Grandview, Man. Woody River, 8 mi N of Swan River, Man. (both this survey).

Nelson River system. Small river north of Petersfield, Man. (this survey).

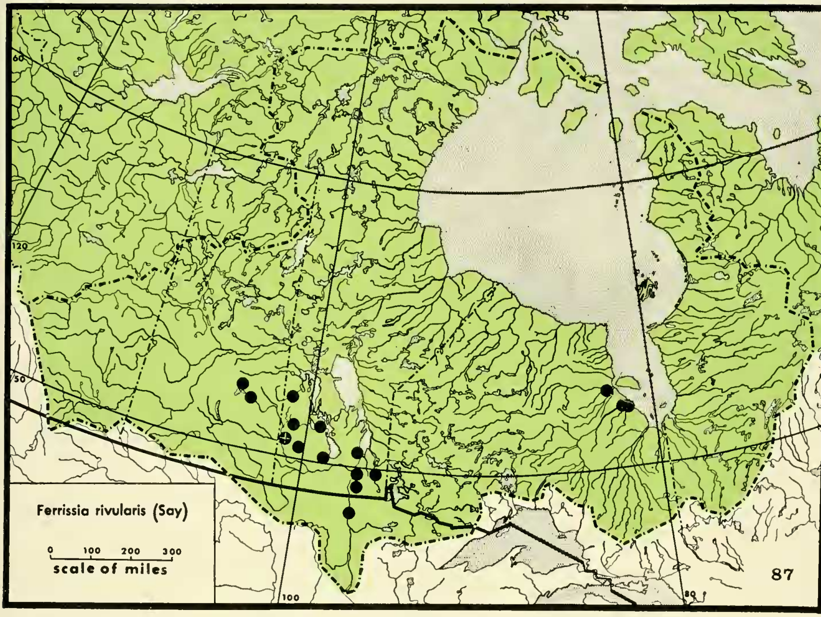
Distribution: Throughout most of North America but exact limits are unknown. It is recorded from as far south as North Carolina (Basch, 1963a: 430) and New Mexico (La Rocque, 1953: 296) and its occurrence in California and Oregon is implied by the synonymy in Basch (1963a: 429). It extends northward into the Hudson Bay Lowlands and northwestward at least to central Saskatchewan. The densest populations seen in this region were in prairie localities, especially in southern Manitoba.

Biology and Ecology: The 14 collections of *Ferrissia rivularis* made during this survey are all from rivers. Seven are from rivers over 100 feet wide, 3 are from rivers 50 to 100 feet wide, and 4 are from rivers 25 to 50 feet wide. Current was slow, medium or fast; vegetation was sparse, moderately abundant, or thick; and bottom deposits were recorded as of all types with mud predominating.

According to Basch (1963a: 430) "the usual habitat of *F. rivularis* is a stream with a gravelly bottom, containing a large proportion of stones at least two inches in diameter. Occasional good collections have been made from earth silt-laden streams with muddy bottom..., but where the silt is finely divided clay that remains in suspension, limpets are invariably absent. *Ferrissia rivularis* is tolerant of organic pollution."

The presence or absence of stones for limpet attachment was not specifically noted during the present survey. I remember well some *F. rivularis* localities in which I am certain that stones were either absent or at least entirely buried by mud, however. *F. rivularis* also often occurs on or in empty freshwater mussel shells.

The anatomy of this species has been described in a preliminary manner by



Baker (1928a: 387 etc.) and in detail by Hoff (1940) and Hubendick (1963: 24-28). The radula formula is approximately 19-1-19 to 21-1-21, with 2 large cusps on the central tooth and 1 minute cusp basally on each side. The 1st laterals have 3 large cusps and 2 small cusps (on the outer edge) which are gradually replaced by 2 large cusps and several small cusps on others nearer the ends of the transverse rows.

Remarks: The distribution of *Ferrissia rivularis* within the Hudson Bay drainage area is similar to that of *Lymnaea elodes*, *Aplexa hypnorum*, and some other species which are rare or absent from the Precambrian Shield but are often abundant in hard-water habitats west (and south) of the Shield and in the lime-rich Hudson Bay Lowlands within the Shield.

Ferrissia parallela (Haldeman)
Plate 28, Figs. 9, 10; Map 86.

Ancylus parallelus Haldeman, 1841: *A monograph of the freshwater univalve Mollusca of the United States*. Pt. 3: cover (not seen); 1844, *Ibid*., Pt. 7: 11, pl. 1: 6. Type locality: "Inhabits New England."

Diagnosis: Shell up to about $\frac{1}{3}$ inch long, elongate, elevated, relatively smooth and aperture with straight, parallel sides. Apex obtuse, in the midline, and very finely striate.

Description: "Narrow, elongated, the lateral margins nearly straight, widening more or less anteriorly, ends well rounded; anterior slope rather long, slightly convex; posterior slope shorter than anterior, straight or but slightly concave; right lateral slope nearly straight, left lateral slope slightly convex; apex sub-acute, slightly turned

toward the right and slightly anterior of the center of the shell; radially striate; lines of growth fine, irregular, but well marked; the peritreme of the shell may be even or it may be concave at both ends, when the habitat has been upon *Scirpus*. Color of shell pale corneous." (Baker, 1928a: 395).

Measurements:

Feature	N	Range	Mean	S.E.$_M$	S.D.
Outlet of Lac Pascalis, 13 mi S of Senneterre, Que.					
Length, mm	3	6·1—6·3	6·22	—	—
Width, mm	3	2·8—3·3	2·97	—	—
Height, mm	3	2·0	2 00	—	—
L/W	3	1·9—2·3	2·10	—	—
L/H	3	3·0—3·2	3·11	—	—
W/H	3	1·4—1·7	1·46	—	—
Klotz Lake, 30 mi E of Longlac, Ont.					
Length, mm	16	3·7—7·6	4·95	—	—
Width, mm	16	2·1—3·2	2·45	—	—
Height, mm	16	1·1—2·7	1·82	—	—
L/W	16	1·8—2·6	2·12	0·06	0·24
L/H	16	2·3—3·6	2·91	0·07	0·27
W/H	16	1·1—2·0	1·39	0·06	0·24

Records:

Nottaway River system. Outlet of Lac Pascalis at Lac Tiblemont, 13 mi S of Senneterre, Que. Bell River, 33 mi N of Senneterre. Lac Doré, 6 mi SE of Chibougamau, Que. (all this survey).

Moose River system. Wilson Lake, 1·5 mi S of Nellie Lake, Ont. Black River, Matheson, Ont. (both this survey).

Albany River system. Lydia Lake, 23 mi E of Longlac, Ont. Klotz Lake, 30 mi E of Longlac. Small stream 30 mi N of Savant Lake, Ont. (all this survey).

Winnipeg River system. Pashkokogan Lake, Ont. (Baker & Cahn, 1931: 60). Small stream 30 mi N of Savant Lake, Ont. Wabaskang Lake, 40 mi N of Vermilion Bay, Ont. (both this survey). "Otter Track Lake", Rainy River District, Ont. (Baker, 1939b: 98). Moth Lake, 25 mi W of Kenora, Ont. (this survey). "Pine Creek; Rainy River; and Lake of the Woods, in Manitoba" (Dall, 1905: 110). Rennie River, near Brereton, Man. Lake Brereton, Man. Whiteshell River, Man. (all Mozley, 1938: 114). Pond 6 mi W of Whitemouth, Man. (this survey).

Distribution: Nova Scotia and New England west to Manitoba, Minnesota, and Illinois in the Atlantic, St. Lawrence River, Hudson Bay, and Upper Mississippi River drainage areas.

Biology and Ecology: The 12 collections of *Ferrissia parallela* made during this survey came from the following habitats: 4 collections are from large lakes, 1 is from a medium-sized lake, 2 are from small lakes, 1 is from a pond about ½ acre in area, 2 are from large, slow-flowing rivers, 1 is from a slow-flowing lake outlet near a large lake, and 1 is from a small, slow-flowing stream amid muskeg. Vegetation was

thick at 5 localities, moderately thick at 5, and sparse at 2. (The 2 last-named localities, a pond near Whitemouth, Manitoba and Lac Doré, near Chibougamau Que. were investigated in June before vegetation had become well developed, however). Bottom sediments were of mud at all localities except Wabaskang Lake, where it was sand, and Bell River, where it was clay.

Basch (1963a: 440) gives its habitat as " on vegetation, particularly *Scirpus*, *Typha*, etc., in shallow lakes [primarily] in clean water but [also] in muddy, turbid water in shallow swamps..."

According to Basch (loc. cit.) the anatomy of *Ferrissia parallela*, including the radula, is very similar to that of *F. rivularis*. Hubendick (1963: 26) has found differences in the reproductive systems, however.

One adult specimen collected in June, 1968 from Lac Doré, Quebec, was observed for 25 days in the laboratory (Clarke, 1969a). Between the 7th to the 25th day after installation it deposited about 12 egg capsules on the sides of the culture dish. It died on the 25th day. The egg capsules contained from 1 to 3 whitish, closely packed eggs each of which was about 1·0 mm long. The outer membrane of the capsules was closely appressed to the eggs and the lumen was white. The cultures were kept at room temperature and about 5 days after oviposition young *Ferrissia*, each about 1·0 mm long, began to emerge.

ADDENDUM

Note added in proof. Since this manuscript was completed another species has been found in the Canadian Interior Basin, viz. *Lymnaea auricularia* L. (also known as *Radix auricularia* (L.)). It was collected in the Bow River at Calgary, Alberta in September, 1971 by Dr. Leonard J. Kalas of the Canada Department of the Environment. *L. auricularia* is a European species which has been widlely introduced in North America. It is figured and discussed by Baker (1913; 179) and Hubendick (1951; 149). I am grateful to Dr. Kalas for making this information available and for the donation of specimens.

NOTE ADDED IN PROOF

Continuing cytological and immunological studies on Lymnaeidae by J. B. Burch, A. Inaba, C. M. Patterson, and others [see review by Patterson, 1969, *Proc. Symp. Moll.*, Mar. biol. Assn. India, Pt. 2, p 635–686; Inaba, 1969, *Malacologia*, 7(2–3): 143–168; Burch, Lindsay & LoVerde, 1971, *Zool. Zh.*, 50(8): 1158–1168] have contributed strong evidence that natural, mutually exclusive, phylogenetic species groups do exist within Lymnaeidae. These groups correspond to *Fossaria*, *Lymnaea* (s.s.), *Radix*, *Stagnicola* and other genus-group names of recent authors. Substantial work remains to be done, e.g. provision of a firm basis for the name *Stagnicola* through designation of a neotype population of *Lymnaea palustris* and further investigation of such " intermediate" species as *Lymnaea atkaensis*. The present state of knowledge is such, however, that use of subgroup names in the conventional sense, and at the subgeneric level under *Lymnaea*, is now considered conservative and correct.

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ZUSAMMENFASSUNG
DIE SÜSSWASSERMOLLUSKEN DES KANADISCHEN INNEREN BECKENS

A. H. Clarke

Das kanadische Innere Becken schliesst sowohl das Hudson-Bay-Becken als auch den kanadischen Teil des "Arktischen Beckens" früherer Autoren ein. Es umfasst mehr als $\frac{1}{3}$ von Nordamerika. Die taxonomische Bearbeitung der in ihm gefundenen Süsswassermollusken, im wesentlichen auf biometrischer Populationsanalyse aufbauend, führte zur Unterscheidung von 37 Gattungen und Untergattungen und 103 Arten und Unterarten.

Die Einleitung bringt einen Überblick ber frühere Arbeiten, Topographie, Geologie, Pleistozängeschichte, zwischen Abfluss-gebieten bestehende Verbindungen, pflanzengeographische Regionen, Klima und verwendete Feldmethoden. Es folgt eine Diskussion der postpleistozänen Herkunft der Faunenelemente, einiger beobachteter Beziehungen zwischen zoogeographischen Befunden einerseits und Temperatur sowie Geologie anderseits, und des Ausmasses des erreichten Verbreitungsgleichgewichts. Der systematische Teil enthält Diskussionen der Taxonomie, Morphologie (mit den Ergebnissen der statistischen Analysen), Zoogeographie, Biologie, Ökologie und der zwischenartlichen Beziehungen aller Arten und Unterarten. Vereinfachte Bestimmungsschlüssel, Verbreitungskarten und Abbildungen (viele davon farbig) aller Arten und Unterarten sind beigegeben. Zahlreiche taxonomische Umstellungen werden empfohlen, und für neue Taxa werden folgende Namen vorgeschlagen: **Herringtonium** (n. subgen. von *Sphaerium*) und **Physa jennessi athearni** (n. ssp.)

C.M.B.

RÉSUMÉ
LES MOLLUSQUES D'EAU DOUCE DU BASSIN CANADIEN INTERIEUR

A. H. Clarke

Le Bassin Canadien intérieur comporte à la fois le "Bassin de la Baie d'Hudson" et le "Bassin arctique" des auteurs précédents. Il comprend plus du $\frac{1}{3}$ de l'Amérique du Nord. Une revision taxonomique des mollusques dulçaquicoles qu'on y trouve, basée principalement sur une analyse biométrique de la population, a conduit à y reconnaître 37 genres et sous-genres et 103 espèces et sous-espèces.

L'introduction continent les résumés de travaux précédents, la topographie, la géologie, l'histoire du Pleistocène, connections existantes entre les aires de drainage, les régions phytogéographiques, le climat et les méthodes de réclots. Ceci est suivi d'une discussion sur les origines post-Pleistocène de la faune, par l'observation de certaines relations entre la zoogéographie et la température, ainsi que la géologie et enfin par l'extension de l'équilibre de distribution qui a été atteint. La Section de Systématique contient des discussions de taxonomie, de morphologie (avec des données statistique) de zoogéographie, de biologie, d'écologie, et de relations interspécifiques entre espéces et sousèspèces. On y trouve des clés simplifiées d'identification, des cartes de distribution et des illustrations (dont beaucoup en couleurs) pour toutes les espèces et sous-espèces. De nombreux changements taxonomiques sont recommandés et les nouveaux noms suivants sont proposés: **Herringtonium** (nouveau sous-genre de *Sphaerium*) et **Physa jennessi athearni** (n. ssp).

A.L.

RESUMÈN
LOS MOLUSCOS FLUVIALES DE LA CUENCA INTERIOR CANADIENSE

A. H. Clarke

La Cuenca Interior Canadiense abarca la " cuenca de la Bahía Hudson " y la parte de la " cuenca Artica " correspondiente al Canadá de previos autores y comprende más un tercio de Norte América. La revisión taxonómica de los moluscos fluviales que allí se encuentran, basada principalmente en un análisis biométrico de las poblaciones, resultó en el reconocimiento de 37 géneros y subgéneros con 103 especies y subespecies.

La introducción contiene un sumario de trabajos previos, topografía, geología, historia del Pleistoceno, las conexiones existentes entre las áreas de desagüe, regiones fitogeográficas, clima, y los métodos usados en campaña. A esto sigue una discusión acerca del origen post-pleistocenico de la fauna, algunas observaciones sobre la relación entre zoogeografia, temperatura y geología, y hasta que punto el equilibrio distribucional se ha consumado. La Sección Sistemática discute la taxonomía, morfología, (con sumarios estadísticos), zoogeografía, biología, ecología, y relaciones interespecificas de todas las especies y subespecies. Claves para simplificar la identificación y mapas de distribución e ilustraciones (muchas en color) se incluyen, de todas las especies y subespecies. Se recomiendan numerosos cambios taxonómicos y se proponon los siguientes nuevos nombres: **Herringtonium** (nuevo subgénero de *Sphaerium*) y **Physa jennesi athearni** (nueva subespecies).

J. J. P.

АБСТРАКТ

ПРЕСНОВОДНЫЕ МОЛЛЮСКИ КАНАДСКИХ ВНУТРЕННИХ ВОД

А. Х. КЛАРК

Внутренние воды Канады включают как "бассейн Гудзонова залива", так и канадскую часть "арктического бассейна"прежних авторов. Это название охватывает более 1/3 всей Северной Америки.

Таксономическая ревизия обитающих здесь пресноводных моллюсков основана, главным образом, на биометрическом анализе популяций, что в результате дало 37 родов и подродов, 103 вида и подвида.

Во введении приводится сводка всех предыдущих исследований, топография и геология района исследования, его история в плейстоценовое время, существующие связи между дренажными районами, фитогеографическое районирование, климатические условия, а также методы полевых исследований.

Эта часть работы сопровождается дискуссией по вопросу о пост-плиоценовом происхождении элементов фауны, о наблюдаемой связи зоогеографических групп с температурой и геологией; рассматривается также степень существующего равновесия в распространении моллюсков. В разделе по систематике обсуждаются таксономия и морфология моллюсков (со статистическими выводами), рассматривается их зоогеография, биология, экология и внутривидовые взаимоотношения всех их видов и подвидов.

Для всех видов и подвидов даются упрощенные определительные ключи, карты распространения и иллюстрации (многие в цвете). Рекомендуется много таксономических изменений, предлагаются следующие новые названия: *Herringtonium* (для нового подрода *Sphaerium*) и *Physa jennesse athearni* (**n. ssp.**).

Z. A. F.

INDEX TO SCIENTIFIC NAMES

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